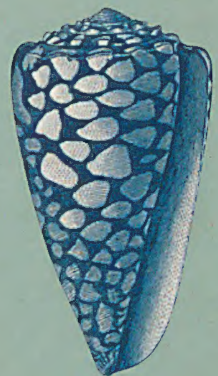

Molluscan Research

Volume 24 • Number 3

The Malacological Society of Australasia

Molluscan Research

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Biology of the golden apple snail, *Pomacea canaliculata* (Lamarck, 1822), with emphasis on responses to certain environmental conditions in Sabah, Malaysia

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Abstract

This study investigated the ecology and biology of the golden apple snail in rice fields. Egg masses were produced at inconsistent intervals with the number of eggs per cluster ranging from 92 to 592 (mean 272). Regardless of clutch size, hatching success ranged from 87 to 100% (mean 95.8%). In the field, mating took place 82 days after hatching. Mean shell length at this age was 38.2 mm with females bigger than males in general. The male to female ratio was ~1: 5. Peat soils reduced egg mass production significantly and egg masses submerged in water for more than 1 week reduced hatching success significantly.

Introduction

The golden apple snail, *Pomacea canaliculata* (Lamarck, 1822), is native to South America. It was introduced from Argentina to Taiwan in the 1980s for commercial production (Mochida 1991) and was distributed widely in Asia as a dietary protein supplement and income earner for the rural poor (Matienzo 1984; Anderson 1993). Unfortunately the introduction of *P. canaliculata* was done in haste without prior studies on its ecological impact or market information (Acosta and Pullin 1989). When market demand for the snail was poor, many snail-farming projects were abandoned and in many instances the snails escaped and subsequently became a pest of crops, mainly rice (Naylor 1996). The snail is now a major rice pest in Asia (Hirai 1988; Rejesus *et al.* 1990; Halwart 1994*a*). The estimated infested area in Taiwan was 171 425 ha in 1986, 16 196 ha in Japan in 1989 and 400 000 ha in the Philippines in 1989 (Mochida 1991). When the golden apple snail began to become a pest, information on its ecology, biology and control measures was lacking. Pesticides were selected rather arbitrarily, applied inappropriately (causing environmental pollution) and were a hazard to public health with farmers suffering a range of health problems (Anderson 1993). Several control techniques have been developed, including biological (Halwart 1994*b*; Teo 2001), cultural (Teo 2003) and chemical (Litsinger and Estano 1993; Palis *et al.* 1994) controls. Information on the biology and ecology of the snail are also becoming available, most recently in a review by Cowie (2002). However, many of these reports are not species specific, with information on *P. canaliculata* sparse and dispersed. A comprehensive understanding of the biology of this species is essential for formulating an effective management strategy. Consequently, studies on the ecology of *P. canaliculata* were initiated in Sabah, Malaysia with a view to developing control measures.

In Sabah the snail is also found in rice fields with peat soils but observations suggest that it does not establish well under these conditions. In the wetlands, many of its egg masses may become submerged in water for several days during the monsoon season. The studies presented here cover growth and reproduction, the influence of water depth on snail mortality, egg submergence and viability, and effect of peat soils on egg mass production.

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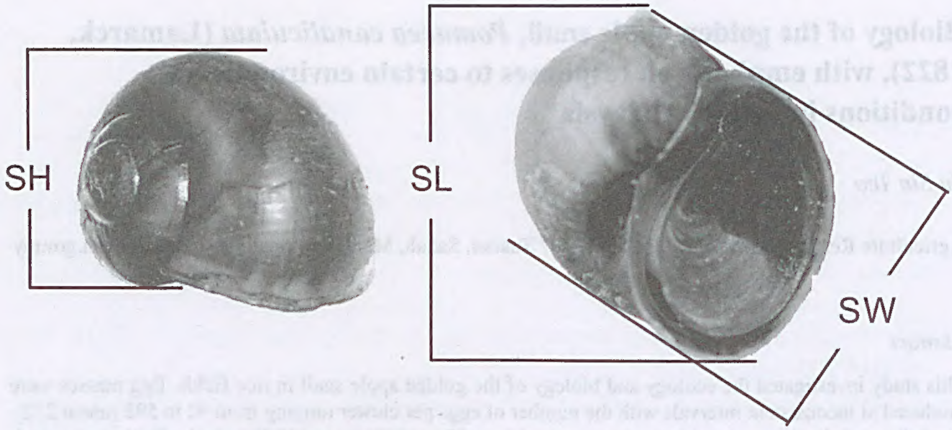

Fig. 1. Measurements of *Pomacea canaliculata* shells. SH, shell height; SL, shell length; SW, shell width.

Materials and methods

General

Unless otherwise stated, all experiments were conducted at the Agriculture Research Centre, Tuaran. The experimental plots were all separated by bunds made of mud from the field with width 150 mm and height 200 mm. The water in the plots and fibreglass bin was maintained at 50–100 mm depth and planted with water spinach (*Ipomea aquatica* Forsk) as feed for the snails.

Shell size and sex ratio

Snails were collected at random in rice fields during the paddy-planting season in a few villages in each of the districts of Tuaran, Tambunan and Keningau, these being the main snail-infested areas. The villages are a few kilometres apart but the districts are at least 150 km away from one another. The study was carried out when the crop was ~45 cm high, just before the booting stage. The snail population density was low at the time of the study because of control measures applied by the farmers, so a larger sample would have been difficult to collect. Each sample consisted of at least 20 adult snails. Figure 1 shows the shell dimensions taken using a digital Vernier caliper.

Number of eggs per cluster

Pomacea snails lay their eggs on objects protruding above the water surface. One hundred and thirty egg masses were collected at random from the rice fields in Tuaran during the rainy season, coinciding with the breeding season of the pest. The number of eggs per mass was counted manually by separating them one by one with a needle.

Growth increment – indoor and field conditions

A fibreglass bin (0.9 m × 1.2 m × 2.4 m) was used in the indoor studies. The bin was filled with 300 mm of mud collected from the rice field. An egg cluster laid on a stick was collected from the field and was staked into the mud in the bin and allowed to hatch. Growth rate measurements were initiated 3 weeks after egg hatching when the snails were easier to handle without damage. Only ten snails were kept in the bin, excess snails were discarded. The field study was conducted in the rice field in a 1 m × 2 m plot without the paddy plants during the rainy season. An egg cluster collected from the field was staked onto the plot and allowed to hatch. Only ten snails were kept in each plot to prevent overcrowding. Shell measurements were taken daily with a digital caliper and later weekly when growth began to plateau. At each measurement event, the length, width and height (see Fig. 1) of ten snails were recorded. Growth under higher population density was also measured, in a 2 m × 2 m plot under similar environmental conditions.

Pattern and frequency of oviposition

The objective of this part of the study was to investigate the pattern of egg mass production. Single female snails in each of fourteen plots of 1 m × 1 m were observed, each collected from the field and with a shell height of ~25 mm. Each of the plots was fenced with wire mesh to a height of 600 mm to keep the snails confined. The number of egg masses produced was recorded daily for a period of 5 months.

Hatching rate

Fifty egg masses were collected at random from the rice field at the Research Centre during the breeding season. Each egg mass was placed above 5 mm of water in a beaker, and then allowed to hatch. When hatching was complete, the number of hatchlings and unhatched eggs were counted and the percentage hatched was calculated.

Effect of peat substrate on egg mass production

The objective of this part of the study was to investigate the effect of peat on egg mass production. The plots were prepared by removing the rice stubble followed by ground levelling. Five plots, each measuring 1 m × 2 m were prepared and peat soil was laid across the plot at 25, 50, 75 and 100 mm depths. One plot was untreated and served as a control. Rice was not planted in the plots and the experiment was not replicated. The peat substrate was collected from a rice field in Sipitang (200 km away from the Research Centre) at depths of 0–150 mm. This area is covered by fibrous peat consisting of undecomposed or partly decomposed woody plants with a pH of 3.5 (Bower *et al.* 1975). A total of 30 adult snails (20 female and 10 male) with a shell height of 25 mm were collected from the rice field and introduced into each plot. Stakes were placed in each plot for the snails to oviposit their eggs. Recordings were made daily for a period of 2 months.

Egg mass production and mortality of snails under different depths of water

The objective of this experiment was to determine egg mass production and snail mortality under different depths of water. Five plots (1 m × 2 m) were prepared, each with a water depth of 50, 300, 600, 900 or 1200 mm. The experiment was not replicated. Fifteen adult snails (shell height 25 mm) with a male to female ratio of 1 : 5 were introduced into each of the plots. Sticks were placed vertically into the plots for the snails to oviposit their eggs. The number of egg masses produced and the number of snails that died over time were recorded for 3 months. After this period, the water in the plots was removed using a water pump and the number of snails surviving in each plot was recorded. Water temperatures at each depth were recorded at 8:00 am, 12:00 pm and 3:00 pm on Monday, Wednesday and Friday in alternate weeks.

Hatching success of Pomacea canaliculata *egg masses immersed in water for different lengths of time*

The objective was to investigate the viability of egg masses after they were submerged in water for different lengths of time. A randomised design was adopted with five replicates, consisting of five egg masses per replicate. Egg masses of approximately the same size were collected from the field, with the colour giving their approximate age. Newly laid egg masses are bright pinkish-red in colour, which fades to light pinkish and then greyish before hatching. Only pinkish egg masses of approximately the same colour were selected. The egg masses were submerged in water for 0–14 nights. After each treatment, the egg masses were removed from the water and placed above 5 mm of water in a beaker for 21 days. The numbers of hatched and unhatched eggs were recorded.

Results

Shell size and sex ratio

Table 1 shows the shell size and sex ratio of snails sampled from seven different locations. The interaction between sex and shell dimensions was not significantly different. When the mean length, width and height were pooled, females were significantly bigger than males ($F_{1,30} = 14.88$; $P < 0.001$) with overall means of 27.32 ± 1.77 mm and 24.49 ± 1.81 mm respectively. Females were more numerous in the samples than were males, with an overall male to female ratio of 1 : 4.6. The number of males sampled in the studies ranged from 1 to 12 whereas females ranged from 15 to 41.

Table 1. Shell size and sex ratio of *Pomacea canaliculata*

Location	Length (mm)		Width (mm)		Height (mm)		Sample size (n)	Male : female
	Male	Female	Male	Female	Male	Female	male/female	ratio
Marabahai, Tuaran	35.63 ± 1.58	37.53 ± 1.32	30.04 ± 1.33	31.66 ± 1.17	21.02 ± 1.11	23.62 ± 1.03	12/38	1:3.2
Batangan, Tuaran	34.53 ± 1.58	37.37 ± 1.30	28.10 ± 1.41	34.03 ± 1.33	20.44 ± 1.31	22.95 ± 1.09	9/41	1:4.6
Tanaki, Tambunan	28.05 ± 2.71	32.41 ± 1.59	17.55 ± 2.04	19.42 ± 1.16	16.08 ± 2.17	19.71 ± 1.25	3/17	1:5.7
Kiawayan, Tambunan	35.14 ± 3.03	36.21 ± 1.51	20.12 ± 2.25	22.78 ± 1.19	19.25 ± 2.40	21.97 ± 1.20	3/17	1:5.7
Pupuluton, Tambunan	36.31 ± 3.34	35.89 ± 1.53	22.70 ± 2.29	22.91 ± 1.19	21.62 ± 2.31	23.55 ± 1.15	3/17	1:5.7
Lingkodou, Keningau	32.85 ± 1.95	35.15 ± 1.24	19.45 ± 1.51	21.13 ± 0.92	19.09 ± 1.56	21.39 ± 0.87	5/15	1:30
Gasabon, Keningau	25.39 ± 0.00	33.06 ± 1.90	15.74 ± 0.00	20.75 ± 1.50	15.12 ± 0.00	20.18 ± 1.57	1/19	1:19
Mean	32.56 ± 1.19	35.37 ± 0.55	21.96 ± 1.35	24.67 ± 0.94	18.95 ± 0.91	21.91 ± 0.49	5/23	1:4.6

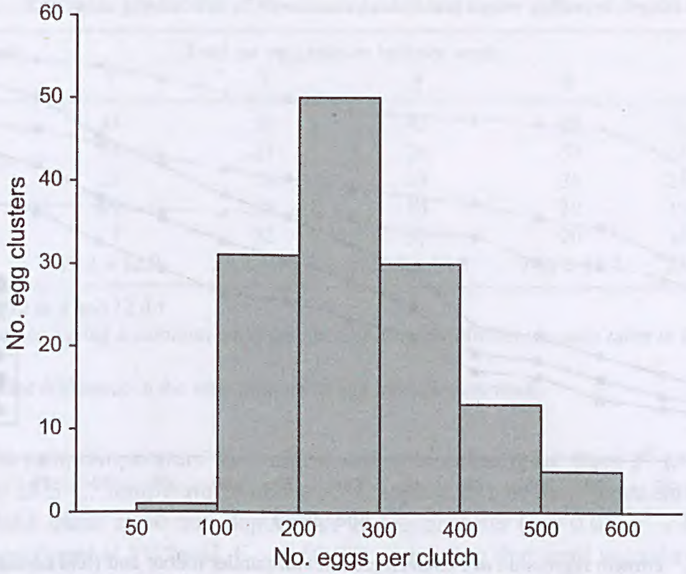

Fig. 2. Clutch size of *Pomacea canaliculata*.

Number of eggs per egg cluster

Figure 2 shows the distribution of the number of eggs per egg mass, which ranged from 92 to 592, with a mean of 272 ± 4.3. Most egg masses had more than 200 eggs, and egg masses with fewer than 100 eggs were rare. Egg masses with 500–600 eggs were not uncommon.

Growth increment – indoor and field conditions

The snails indoors grew faster than those in the field. For the indoor snails at Day 20, the length, width and height of snails kept in the bin indoors were 23.64 ± 0.60 mm, 15.56 ± 0.62 mm and 14.28 ± 0.45 mm respectively. At the corresponding age, those in the field were 6.06 ± 0.48 mm, 4.66 ± 0.50 mm and 3.95 ± 0.40 mm respectively. After Day 60, snails exhibited a continuous pattern of growth with no significant difference in growth rate under both conditions (Fig. 3). Mating was observed at Day 82 under both conditions. At this age, the length, width and height of the snails in the field were 38.2 ± 1.12 mm, 32.60 ± 1.01 mm and 26.5 ± 0.94 mm, and those of the indoor snails were 36.25 ± 0.49 mm, 30.0 ± 0.81 mm and 22.53 ± 0.41mm respectively. In contrast, in the field study, with a population density of at least 20 snails per 30 cm^2, growth was slower and no mating was observed at Day 82. At Day 82, the length, width and height of the snails were only 22.88 ± 0.91 mm, 19.11 ± 0.93 mm and 16.09 ± 0.76 mm respectively.

Pattern and frequency of oviposition

The observational study yielded no consistent pattern of oviposition among the females. Some females laid egg masses once a week for five consecutive weeks, after which they would either stop or continue to lay one or two egg masses per week. Some produced two to four egg masses per week and stopped for two to four weeks but began to lay eggs again after this period. The majority of the snails laid once a week; it was not uncommon for two egg masses to be produced per week. The number of eggs laid per clutch was typically 300–400.

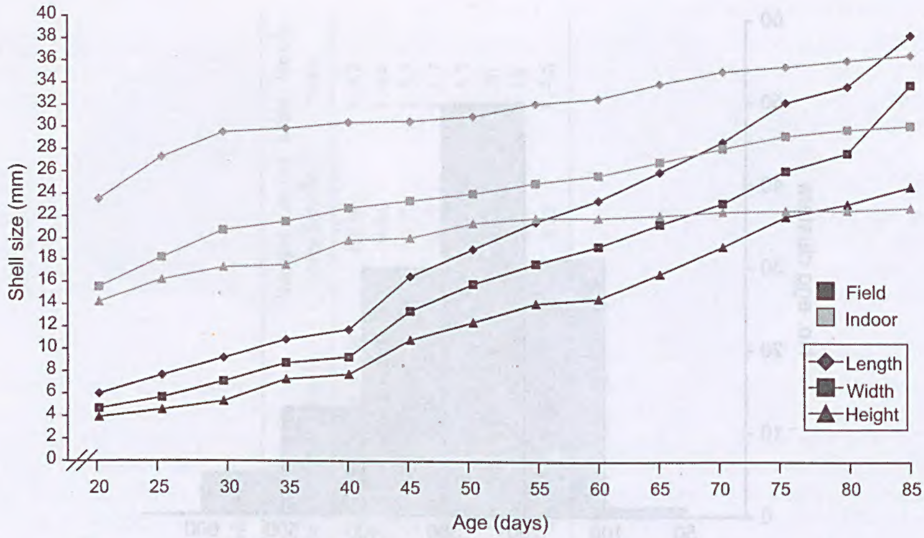

Fig. 3. Growth regression of *Pomacea canaliculata* under indoor and field conditions.

Hatching success

The eggs collected from the field took approximately ~8–12 days to hatch under laboratory conditions, with hatchlings ~2 mm in diameter. Hatching success was high, ranging from 87 to 100% (mean 95.8 ± 0.95%). Hatching rate was not dependent on clutch size; clutches of 127, 140, 148, 477, 512 and 540 eggs produced 89.4, 98.6, 99.3, 97.2, 99.4 and 94.9% hatchlings respectively.

Effect of peat soil on egg mass production

Table 2 shows the number of egg masses laid under different thicknesses of peat. There was a strong relationship between the number of egg masses laid and the thickness of peat placed in the plots. The greater the amount of peat the lesser the number of egg masses produced (fitted regression line $y = 33.35 - 4.85x$ with $r = 0.84$, F-value 15.60, significant at the 5% level). Analysis of variance showed the number of egg masses produced in all the plots treated with peat soil was significantly less than the control ($F_{4,12} = 7.04$; $P = 0.004$). The pH of the water in the plots taken at the end of the trial ranged from 6.1 to 6.7 with a mean of 6.4. These were close to the pH in the normal plots with a range of 5.9–6.4 and a mean of 6.2.

Egg mass production and mortality of snails under different depths of water

The numbers of egg masses produced at water depths of 50, 300, 600, 900 and 1200 mm were 1, 3, 11, 20 and 3, and the percentage snail mortality at the same water depths were 53.3, 26.7, 20.0, 40.0 and 66.7% respectively. While there was a tendency for higher egg mass production at 600 and 900 mm depths, the fitted quadratic regression for the number of egg masses (y) produced and water depth (x) ($y = 0.0035x^2 + 0.051x - 4.43$ with $R^2 = 0.62$) was not significant at the 5% level. Water temperatures might have caused a harmful effect on the snails. At 8:00 am, the difference in temperature was not significant among the water depths, ranging from 27 to 29°C. But at 12:00 pm and 3:00 pm, the temperature at 50 mm depth increased to a mean of 33°C (range 27.5–38°C). At a water

Table 2. Egg mass production of *Pomacea canaliculata* under different depths of peat

Depth of peat soil (cm)	Total no. egg masses laid per week 1	2	3	4	Mean[A]
0	35	39	43	28	36.3 ± 10.2[a]
2.5	14	21	26	37	24.5 ± 15.4[b,c]
5.0	22	26	28	26	25.5 ± 4.0[b]
7.5	19	18	15	10	15.5 ± 6.4[c]
10.0	7	22	17	20	16.5 ± 10.6[b,c]
Mean[NS]	19.4 ± 12.9	25.2 ± 10.2	25.8 ± 13.8	24.2 ± 12.4	23.7 ± 4.5

[A]l.s.d.$_{0.05}$ = 9.72 at 4 and 12 d.f.
[a–c]Any two means having a common letter are not significantly different to each other at the 5% level by l.s.d.
[NS]No significant difference in the total number of egg masses each week.

depth of 1200 mm, temperature fluctuation was minimal ranging from 27 to 30°C with a daily mean of 28.5°C. Temperatures above 30°C appeared to be detrimental to snails. There were more dead snails at 50 mm depth than in deeper water ($y = 0.012x^2 - 1.29x + 57.9$, $R^2 = 0.97$; significant at 5% level, $F_{2,2} = 60.98$), indicating that snail mortality was related to water depth, presumably due to heating.

Hatching success of golden apple snail egg masses after submergence in water for different periods

Table 3 shows the percentage hatching of egg masses after being submerged in water for different lengths of time. The fitted regression line was $y = 92.2 - 5.28x$ (significant at $P < 0.01$, $F_{1,13} = 80.13$, $r = 0.93$). The viability of the egg masses decreases as the duration of submersion increases. There were significant differences in percentage hatching among the treatments ($F_{14,56} = 17.08$; $P < 0.01$). There were no significant differences at the 5% level in percentage hatching with submergence up to 7 days. From Day 8 to Day 14, percentage hatching was significantly lower than in the first 7 days ($F_{14,56} = 17.08$; $P < 0.01$). At Day 14, percentage hatching was lowest, which was significantly different ($F_{14,56} = 17.08$; $P < 0.01$) from Days 0 to 13.

Discussion

Pomacea canaliculata produces numerous egg masses in areas it infests. The range of the number of eggs per egg mass was considerable, reflecting differing sizes of females (Estoy *et al.* 2002). Variability in snail size is partly related to environmental conditions, as high population density and low food availability can lead to smaller shell size and smaller egg masses (Tanaka *et al.* 1999). Diet can also affect clutch size (Lacanilao 1990).

Our samplings for estimates of ratio were done during field visits at various times of the year. The male to female ratio seemed to be consistent at approximately 1 : 5. This is possibly because of insignificant variation of climate in this region, as Banpavichit *et al.* (1994) reported that the sex ratio differed under distinctly different weather patterns. The abundance of egg masses produced in infested areas seemed to indicate that males were able to serve the larger female population successfully. The average shell height of *P. canaliculata* in Sabah is ~25 mm, with females generally larger than males. Males were often seen mating with larger sized females.

Growth was influenced significantly by environmental conditions. Snails cultured indoors grew faster than those in the field in the earlier stages probably because of better,

Table 3. Hatching percentage of *P. canaliculata* egg masses after submerging in water for varying periods

Data are mean ± s.d., with $n = 5$ and $t_{0.05} = 2.78$ at 13 d.f. Square root transformed means have cv = 15.2% and s.d. = 1.08

Period of submergence (days)	Hatching %	Hatching Square root transformed mean
0	91.8 ± 1.93	9.58^{a}
1	73.0 ± 4.42	8.47$^{a–c}$
2	77.6 ± 3.73	8.79^{a,b}
3	67.9 ± 5.86	8.08$^{a–d}$
4	78.7 ± 3.61	8.86^{a,b}
5	79.2 ± 4.62	8.85^{a,b}
6	53.1 ± 5.39	7.13$^{c–e}$
7	67.0 ± 3.73	8.16$^{a–d}$
8	64.6 ± 5.03	7.93$^{b–d}$
9	48.3 ± 4.47	6.86^{d,e}
10	42.2 ± 4.02	6.43^{e}
11	39.0 ± 4.49	5.94^{e,f}
12	15.8 ± 4.18	4.65^{f,g}
13	22.7 ± 4.16	4.43^{g}
14	7.10 ± 2.57	2.50^{h}

[a–h]Any two means having a common letter are not significantly different to each other at the 5% level by Duncan's Multiple Range Test.

more constant conditions (water changed frequently, food not limiting, more constant temperature). At around Day 80, growth of the indoor snails and those in the field was about the same and beginning to plateau (Fig. 3). The study showed that snails in water depths greater than 90 cm had high mortality and low egg mass production. Egg mass production was also low under peaty soil conditions. However, because these were non-replicated experiments, more studies are required to confirm the results. Whether this effect is simply due to lower pH or to substances in the peat detrimental to the snails is presently not known and requires further investigation.

Frequency of oviposition was highly variable but, because of their large numbers in the field, numerous egg masses were produced. Females kept alone in an isolated plot could lay more than once because they had the ability to store sperm (Miyahara *et al.* 1986). In Sabah, oviposition coincides with the rainy season with egg masses very abundant after heavy rain. When the dry weather returns, the number of egg masses decreases gradually. Under prolonged drought, egg masses were completely absent in the field.

During the rainy season, floods are common and many egg masses become submerged. Our results suggest submergence is not detrimental to the egg masses under natural conditions because in Sabah, floods rarely last for more than 1 week. Our study showed that submergence was potentially harmful only when it lasted for more than this period of time.

Conclusions

Pomacea canaliculata thrives under the climatic conditions in Sabah. The snail is prolific and is undoubtedly going to spread throughout the country, if not all of Borneo. It can continue to breed for as long as water is not limiting. In Sabah the dry season is short, so there is a tendency for the snail to increase in number. Growth and reproduction are not the same in different regions. The review by Cowie (2002) indicates that *P. canaliculata* in the

Philippines behaves in a similar way to the snails in Sabah, but in Japan and Argentina the snails take a longer time to reach maturity, hatching success being lower with fewer eggs in each cluster. In Argentina it took 7 months to 2 years for snails to mature (Estebenet and Cazzaniga 1992). In Hawaii a sex ratio of 1 : 1 and a maximum shell size of only 30 mm was reported by Cowie (2002), whereas in Thailand the shells can reach at least 65 mm in height (Keawjam and Upatham 1990).

Apart from being able to thrive in wet places, there are also conditions unfavourable for *P. canaliculata*. The snails cannot tolerate high water temperatures. At water depths of 5 cm with a mean temperature of 33°C mortality was high. Mochida (1991) also reported that temperatures greater than 32°C resulted in high mortality. Snails on peat soils also show a significant reduction in egg mass production.

The adaptability of *P. canaliculata* is not confined to South-East Asia, but to any place with wetlands and warm climate. Baker (1998) reported that several parts of Australia (particularly northern Australian wetlands), parts of North America, Europe, New Zealand and a few Pacific Islands are suitable for the pest to establish. Once infested, the situation is seemingly irreversible. Thus, applying strict quarantine measures at the ports of entry is the best control measure for countries still free of this pest.

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Discovery of the Indo-Pacific oyster *Hyotissa hyotis* (Linnaeus, 1758) in the Florida Keys (Bivalvia: Gryphaeidae)

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Abstract

Recent collections from a shipwreck in ~30 m depth off the Florida Keys recovered an exceptionally large gryphaeid oyster that was identified on morphological grounds as *Hyotissa hyotis* (Linnaeus, 1758), a common constituent of Indian and Pacific Ocean near-shore faunas. This identification was confirmed by molecular characterisation: the Florida specimen had an almost identical large mitochondrial ribosomal subunit (16S) genotype to that obtained from a western Pacific (Guam) conspecific, differing in only two nucleotide positions that were heteroplasmic in the Guam specimen. Although this species has been variously cited to occur in the western Atlantic, careful examination of these records revealed them to be misidentifications of *Hyotissa mcgintyi* (Harry, 1985), originally described from south-eastern Florida. Because *H. hyotis* is much larger than any other regional oyster, it is unlikely to have been overlooked in earlier biotic surveys. It is therefore likely that this specimen, and another recently discovered off West Palm Beach, Florida, stem from a recent undocumented introduction to the western Atlantic.

Additional keywords: 16S rDNA, heteroplasmy, introduced species, Mollusca, North America, western Atlantic.

Introduction

The western Atlantic is home to numerous oyster species, with members of the ostreid genera *Ostrea* Linnaeus, 1758 (introduced), *Crassostrea* Sacco, 1897, *Cryptostrea* Harry, 1985, *Dendostrea* Swainson, 1835, *Ostreola* Monterosato, 1884 and *Teskeyostrea* Harry, 1985, occurring off the western Atlantic coast of the United States (Turgeon *et al.* 1998; Kirkendale *et al.* 2004). Two species of Gryphaeidae have also been reported: *Neopycnodonte cochlear* (Poli, 1795) and *Parahyotissa mcgintyi* Harry, 1985 (Turgeon *et al.* 1998: 32; now placed in *Hyotissa* Stenzel, 1971, see below). Extant gryphaeids differ from ostreids in having more complex larval hinge dentition, a round adductor muscle scar, a ventricle that is penetrated by the rectum, a vesicular shell structure (that appears cellular or spongy under magnification), and so-called vermicular chomata, small rounded, sinuous shell ridges near the ligament on the anterior and posterior margins of both valves (Ranson 1941, 1967*a*, 1967*b*; Stenzel 1971; Torigoe 1981; Harry 1985).

Of the two recognised gryphaeids in this region, *Neopycnodonte cochlear* extends into deep water (with reports to 2100 m) and forms a white to pink to orange, thin, moderately sized (to 7 cm) shell comprised of a deeply cupped left and a flat right valve, and with a geographic range including the eastern and western Atlantic and the Indo-West Pacific (Harry 1986*a*; Carriker and Gaffney 1996). *Hyotissa mcgintyi* (Figs 1, 2) has a cream-coloured to lavender robust shell, more or less circular in outline, usually not exceeding 7–9 cm in height; a saw-toothed shell margin is often developed; its range

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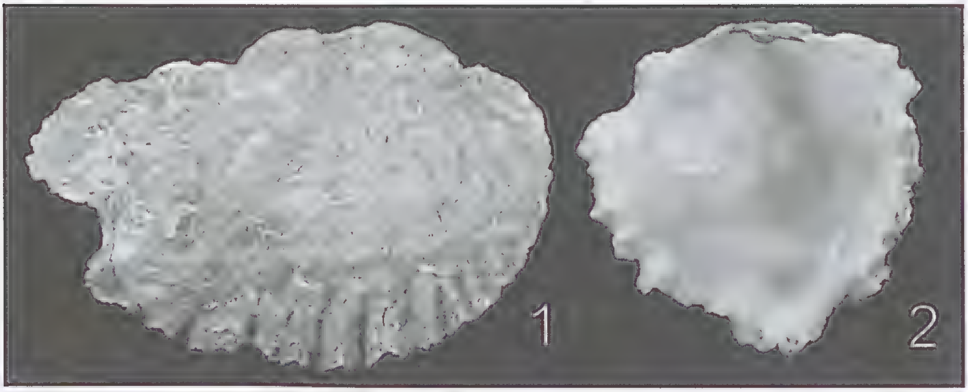


Figs 1, 2. *Hyotissa mcgintyi*, Florida Keys (FMNH 302057). *1*, Outside of free valve, 87 mm greatest shell length; *2*, inside of free valve, 56 mm greatest shell length; note light-coloured margin.

includes the tropical eastern and western Atlantic (Carriker and Gaffney 1996), extending into the northern Gulf of Mexico and to North Carolina. A recent study involving nuclear (28S) and mitochondrial (16S) genes (Kirkendale *et al.* 2004) suggested that there is no phylogenetic basis for recognising *Parahyotissa* Harry, 1985, and proposed the placement of all hyotissinine taxa in the genus *Hyotissa* Stenzel, 1971, a recommendation here followed.

Hyotissa mcgintyi was originally described as *Ostrea thomasi* McLean, 1941, from a single specimen dredged off Palm Beach, south-eastern Florida. It was subsequently considered a synonym of the Indo-Pacific *Hyotissa* (or *Pycnodonte*) *hyotis* (Linnaeus, 1758) by various authors, including Abbott (1974). The name of the supposed senior synonym, *Hyotissa hyotis*, thus became generally used for the larger gryphaeid in the western Atlantic (e.g. Odé 1980). Also known as the honeycomb oyster or giant coxcomb oyster, *Hyotissa hyotis* is one of the largest oysters in the Indo-Pacific, reaching a shell diameter of ~30 cm (Saville-Kent 1893). It is the type species of *Hyotissa*.

In a review of worldwide oyster classification, Harry (1985) introduced a new generic name, *Parahyotissa*, for *Ostrea thomasi*. Recognising that the latter name was preoccupied by *Ostrea sellaeformis* var. *thomasii* Glenn, 1904 (a *nomen nudum* by Conrad, from the early Miocene of Maryland), he introduced a new name, *Parahyotissa mcgintyi*, for the species, and demonstrated morphological/anatomical differences between it and the Indo-Pacific *H. hyotis*. Harry (1985, 1986*a*, 1986*b*) re-identified western Atlantic records of larger-shelled gryphaeids (including those of Odé 1980) as belonging to *P. mcgintyi* and regarded *H. hyotis* as restricted to the Indo-Pacific. Subsequent lists thus excluded *H. hyotis* from the United States coastal fauna (Turgeon *et al.* 1998) and from the western Atlantic oyster fauna (Carriker and Gaffney 1996). The species was not found in a multi-year field/literature/collections survey of Florida Keys bivalves (Mikkelsen and Bieler 2000), and was not collected during a recent (2002) targeted oyster study in the middle Florida Keys by Kirkendale *et al.* (2004).

Nevertheless, the name *Hyotissa hyotis* had remained in post-1985 use in the western Atlantic fauna. Some sources, such as popular shell books and shell dealer listings, continued maintaining it as a cosmopolitan/circumtropical species. This might in part stem from Abbott's earlier (1974) synonymy of *Ostrea thomasi* (= *H. mcgintyi*) under the name of the Indo-Pacific form. In all cases in which we were able to confirm the identity of the

material in question, Atlantic records have been based on individuals of *H. mcgintyi*, not *H. hyotis*. A case in point is Rosenberg's (1992: 138) reference to *H. hyotis* as having circumtropical distribution: the Atlantic record is based on a specimen of *H. mcgintyi* (1992: 138, lower right figure; Grand Bahama Island, ANSP 371816; G. Rosenberg, personal communication). Published records of *H. hyotis* from the Brazilian coast, e.g. that of Celso Guimarães Prado (1996) from Maranhão State, and specimens acquired under that name from Brazilian shell dealers (FMNH 302056) from Bahia State, are likewise specimens of *H. mcgintyi*. The same is the case with the Cuban record of *H. hyotis* by Espinosa and Juarrero (1989), which was subsequently (Espinosa *et al.* 1994) corrected as referring to *H. mcgintyi*. Mexican records of *H. hyotis* refer to material from Baja California Sur (Sevilla-H. *et al.* 1998) and this species has long been documented as a member of the eastern Pacific fauna, previously as *Ostrea fischeri* Dall, 1914 (now regarded as a junior synonym of *H. hyotis* (see Harry 1985)).

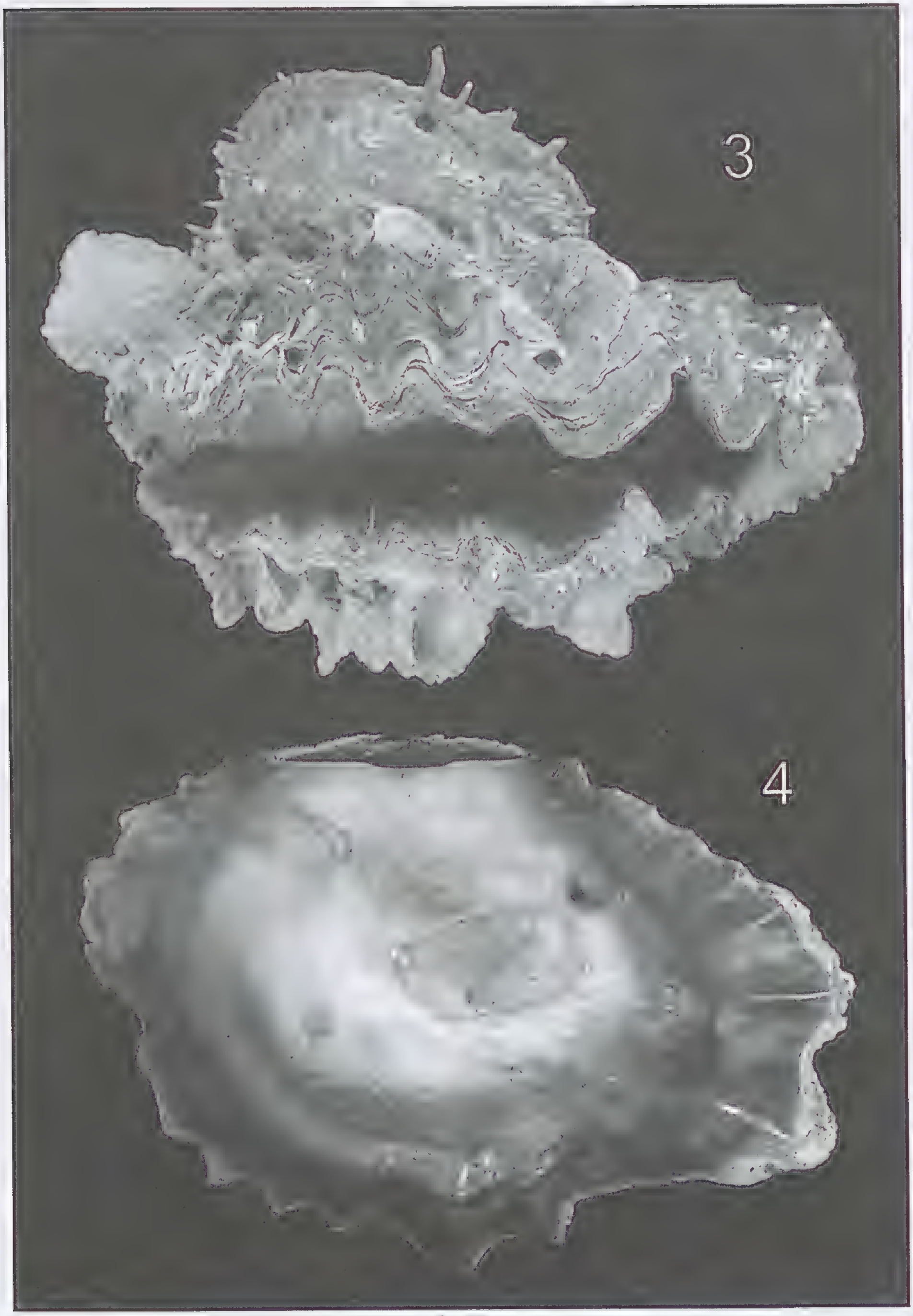
Recent collecting of cemented bivalves on a shipwreck off the middle Florida Keys brought to light an exceptionally large living oyster (Figs 3, 4; 18 cm greatest shell length) that differed greatly from the simultaneously collected *H. mcgintyi* specimens in its size, shell thickness, black shell pigmentation, and black mantle tissue. Its overall morphological appearance is very close to that of *H. hyotis* specimens from the Indo-Pacific and prompted revisiting the question of *H. hyotis*' presence in the western Atlantic. This note serves to establish its species-level identity by molecular phylogenetic analysis and to explore distinguishing shell characters between the two western Atlantic *Hyotissa* species (Table 1).

Materials and methods

The *Hyotissa hyotis* specimen (FMNH 302010) was collected during a scuba survey of bivalves that were part of the fouling community on the steel wreck of the research vessel 'Thunderbolt', off the middle Florida Keys (station FK-717, 19 Aug. 2003, about six nautical miles south of Marathon, 24°39.68′N, 80°57.82′ W, 29–35 m, R. Bieler, A. Bieler & P. Sierwald, coll.; same site collected as station FK-650 on 27 July 2002). The 200-foot ship was intentionally sunk on 6 March 1986, as part of the Florida Keys Artificial Reef Association project, and now lies intact and upright on a sand bottom in ~37 m of water. The specimen of *H. hyotis* formed the basis of a large cluster of fouling and encrusting organisms, including a large living specimen of *Spondylus americanus* Hermann, 1781, and numerous living individuals of *H. mcgintyi* and *Chama congregata* Conrad, 1833. Comparison was made with Indo-Pacific specimens of *H. hyotis* in the AMNH and FMNH collections.

A 95% ethanol-preserved tissue sub-sample of the Floridian *Hyotissa hyotis* specimen (FMNH 302010) was forwarded to the Museum of Zoology, University of Michigan. Total genomic DNA was obtained from 20–30 mg of mantle tissue using a Qiagen extraction kit (Valencia, CA, USA), from which a 492 nucleotide fragment of the mitochondrial large subunit ribosomal gene (16S) was amplified via the polymerase chain reaction using the Kessing *et al.* (1989) 'universal' primers 16Sar (5′-CGCCTGTTTATCAAAAACAT-3′) and 16Sbr (5′-GCCGGTCTGAACTCAGATCACGT-3′). A touchdown protocol (Palumbi 1996) was used: after 4 min denaturation at 94°C, the initial annealing temperature of 65°C was decreased by 2°C/cycle (40 s denaturing at 94°C, 40 s annealing and 1.5 min extension at 72°C) until the final annealing temperature (50°C) was reached and subsequently maintained for an additional 30 cycles. The PCR product was gel-purified (1% agarose) and a sequencing template was prepared using a QIAEX QXII Gel Extraction Kit (Qiagen). Direct, cycle sequencing reactions were performed using BigDye Terminator Cycle Sequencing Ready Reaction (Perkin-Elmer/Applied Biosystems, Palo Alto, CA, USA) with the respective original PCR primers for both strands of the amplified product. Sequencing products were electrophoresed at the University of Michigan Sequencing Core Facility. Resulting chromatograms were edited manually by comparing both strands for all taxa using Sequence Navigator 1.0.1 (Applied Biosystems).

The Floridian *Hyotissa hyotis* 16S mitochondrial genotype was added to a pre-existing gryphaeid 16S nexus file (Kirkendale *et al.* 2004), which included a conspecific haplotype from the western Pacific (Fig. 5), after alignment using Clustal X (Thompson *et al.* 1997). This dataset is available upon request from D. Ó Foighil (diarmaid@umich.edu). It was phylogenetically analysed with PAUP* ver. 4.0b10 (Swofford 2002) using the maximum parsimony optimality criterion with *Neopycnodonte cochlear* as the designated



Figs 3, 4. *Hyotissa hyotis*, Florida Keys, 180 mm specimen (FMNH 302010). *3*, Gaping, partly cleaned shell with attached bivalves (*Spondylus americanus* above, *H. mcgintyi* on left and right, *Chama congregata* below); specimen was cemented to ship hull by the hinge region of the upper valve in this image; *4*, inside of free valve; note dark margin and moiré lines on the slightly iridescent surface.

Table 1. Taxonomic framework, locality data, and voucher specimen information for gryphaeid taxa used in this study

Higher grouping	Species	Taxonomic relevance	Sample locality	Museum vouchers	GenBank number
Pycnodonteinae: Hyotissini	*Hyotissa hyotis* (Linnaeus, 1758)	Type (as *Mytilus hyotis*) of *Hyotissa* Stenzel, 1971	Florida Keys, FK-717	FMNH 302010	AY548883
	Hyotissa hyotis (Linnaeus, 1758)	Same as previous	Guam	UMMZ 265995	AY376599
	Hyotissa mcgintyi (Harry, 1985)	New name for *Ostrea thomasi* McLean, 1941; type of *Parahyotissa* Harry, 1985	Florida Keys, FK-650 and FK-717	UMMZ 300092 (for DNA), FMNH 302057, AMNH 308091	AY376597
	Hyotissa numisma (Lamarck, 1819)	Type (as *Ostrea numisma*) of *Parahyotissa (Numismoida)* Harry, 1985	Guam	UMMZ 265996	AY376598
Pycnodonteinae: Neopycnodontini	*Neopycnodonte cochlear* (Poli, 1795)	Type (as *Ostrea cochlear*) of *Neopycnodonte* Stenzel, 1971	Maui, Hawaii	UMMZ 265997	AY376600

```
                   1                                                                                                  100
H. hyotis Guam     CGCCACTCGATTGTCAYGTGTGGTAGTACCTGCCCAGTGCGCGAGATGCGTAAACGGYGGCTGTAACCTGACGGTCCTAAGGTAGCGAAATTCCTAGCCC
H. hyotis Florida  ----------------C----------------------------------------T------------------------------------------
                   101                                                                                                200
H. hyotis Guam     TTTAATTGGGGGCCTGCATGAAGGTTTGACGAGGGCTTCACTGTCTCTTGCCTTGAGAGATTGAAATTTAGTTAGGGGTGCAGACGCCCTTGTAGTAAAG
H. hyotis Florida  ----------------------------------------------------------------------------------------------------
                   201                                                                                                300
H. hyotis Guam     TTAGACAAAAAGACCCCGTGCAACTTTAAAGAGGGGTGCTGGTATTTGAACTCGTCTTATTTTTGGTGGGGCGCCAGGGAAGTATACAAAACCTTCTCT
H. hyotis Florida  ----------------------------------------------------------------------------------------------------
                   301                                                                                                400
H. hyotis Guam     TATAGAAACAACGCGACACGTGATGATCCAAATTTGTTTGAGAATAGGAGAAGTTACGCCGGGGATAACAGAGCAATCCTGCAGTAGAGTCCGTATTAGC
H. hyotis Florida  ----------------------------------------------------------------------------------------------------
                   401                                                                                        492
H. hyotis Guam     TGCGGGGATTGCCACCTCGATGTTGAATTATGGATGATAACTCTTTGGTTGCAGCAGCTATTGAAGTAGGTCTGTTCGACCTTTGAAACCTT
H. hyotis Florida  --------------------------------------------------------------------------------------------
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Fig. 5. Alignment of two *Hyotissa hyotis* mitochondrial large ribosomal subunit (16S) gene fragments. The top sequence was obtained from a western Pacific specimen sampled in Guam (Kirkendale *et al.* 2004) and the bottom sequence is from a western Atlantic specimen sampled in the Florida Keys. Dashes in the latter indicate nucleotide identity to the Guam specimen. Note that in the two positions that vary among the samples, the Guam specimen exhibited a C/T heteroplasmic condition, here represented by a 'Y'.

outgroup (Ó Foighil and Taylor 2000). Analyses were performed using the heuristic search option with 100 random stepwise additions and tree bisection-reconnection (TBR) branch-swapping. Characters were unordered and equally weighted, and inferred sequence gaps were considered as missing data. Branch support levels were estimated with bootstrapping (Felsenstein 1985) (1000 replications, heuristic searches, 10 random additions each).

Institutional acronyms

AMNH	American Museum of Natural History, New York, New York, USA
ANSP	Academy of Natural Sciences of Philadelphia, Pennsylvania, USA
FMNH	Field Museum of Natural History, Chicago, Illinois, USA
UMMZ	Museum of Zoology, University of Michigan, Ann Arbor, Michigan, USA

Results and discussion

Fully grown specimens of *Hyotissa hyotis* are relatively easy to separate from those of *H. mcgintyi*, by simple virtue of size: *H. hyotis* attains a shell length nearly twice that of *H. mcgintyi* (Table 2). The other obvious difference is the dark shell colouration (black in the Florida specimen, black or brown in the Indo-Pacific material), and the black body colouration of *H. hyotis*, both of which are much lighter in *H. mcgintyi*. Internally, shell colouration varies somewhat, but *H. hyotis* was consistently darker closer to the shell margin, while *H. mcgintyi* was consistently lighter and never displayed any black or dark-brown pigment. Both species are irregularly sculptured externally, can have wavy, saw-toothed margins, and of course have the vesicular shell structure characteristic of Gryphaeidae (distinguishing them from other saw-toothed oysters, e.g. *Dendostrea frons* (Linnaeus, 1758), *Ostreola equestris* (Say, 1834)). No juvenile specimens of *H. hyotis* have been available in this study. Thomson (1954) described small Indo-Pacific specimens of what he thought to be *H. hyotis* as having very shallow lower valves, weakly crenulated margins, reddish purple radial lines on the external shell margin, and chalky white or greenish shell interior. However, it must be noted that these supposed *H. hyotis* juveniles were assignable to the nominal species *Ostrea procles* Iredale, 1939, which Thomson (1954: 161) considered synonymous with *H. hyotis*. *Ostrea procles* is now considered a synonym of *Hyotissa numisma* (Lamarck, 1819) (e.g. Lamprell and Healey 1998).

The Floridian specimen of *Hyotissa hyotis* had an almost identical 16S mitochondrial genotype to that obtained from a western Pacific (Guam) conspecific by Kirkendale *et al.* (2004), differing in only two nucleotide positions (Fig. 6). Interestingly, both variable positions were heteroplasmic in the Guam specimen: two nucleotide peaks (C/T) in the same position on both DNA strands. The Floridian specimen had a clean C and a clean T

Table 2. Comparison of shell features of Florida *Hyotissa* species

	Max. shell diameter	Margin	External colouration	Internal colouration
Hyotissa hyotis	To 18 cm (single specimen)	Wavy, large saw-toothed	Purplish black	Dirty bluish-white in centre to bluish black toward margin (reminiscent of *Pinctada margaritifera* (Linnaeus, 1758))
Hyotissa mcgintyi	To 10 cm	Irregular or saw-toothed	Cream, pinkish or lavender	Cream, pinkish, dirty light brown; in fresh specimens lightest coloured area often near shell margin

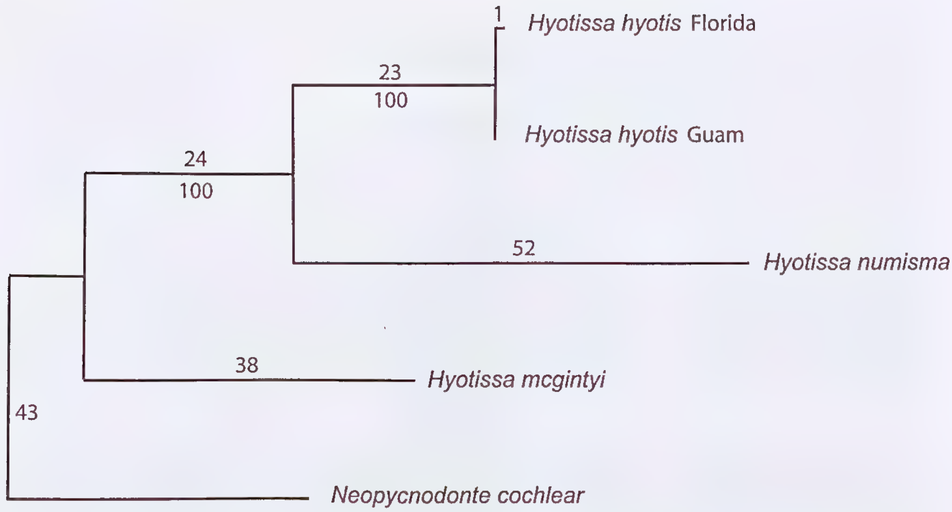

Fig. 6. Most parsimonious tree (173 steps, $CI = 0.948$, $RI = 0.824$) obtained by an exhaustive search for optimal trees (PAUP*) of available gryphaeid mitochondrial 16S genotypes (Table 1). *Neopycnodonte cochlear* was the designated outgroup, characters were unordered and equally weighted, and inferred sequence gaps were considered as missing data. Respective number of steps is indicated above each branch and the bootstrap values (Felsenstein 1985) supporting each node are presented below the branches.

in homologous sites. These ambiguous positions in the Guam specimen were coded as 'Y' (pyramidine) in our analyses and it appears that this *H. hyotis* individual contained multiple mitochondrial 16S genotypes, one of which could be identical to that of the homoplasmic Floridian conspecific. Mitochondrial heteroplasmy, in the form of Doubly Uniparental Inheritance (DUI; Zouros *et al.* 1994) systems, has been documented in several distinct bivalve clades (Skibinski *et al.* 1994; Hoeh *et al.* 1996; Liu *et al.* 1996; Passamonti and Scali 2001). To our knowledge, DUI has yet to be demonstrated in oysters, so the significance of the apparent mitochondrial heteroplasmy in the Guam *H. hyotis* individual remains to be established. Phylogenetic analysis of the gryphaeid mitochondrial 16S dataset placed the Floridian *H. hyotis* specimen in a robust, shallow tip clade with its Guam conspecific (Fig. 4) and unambiguously corroborated its initial taxonomic identification based on conchological features.

Neither *Hyotissa* species appears to be common in south-eastern Florida waters, (probably due to the lack of suitable 'hard-bottom' substrata, apart from shipwrecks), but *H. mcgyntyi* has well established regional populations in the Gulf of Mexico. It is 'abundant on the offshore coral reefs off Texas and locally almost reef forming on Miocene shale outcrops' according to Odé (1980: 49, as *Pycnodonte hyotis*), and has been collected since the 1960s (with the popularisation of scuba diving) from deeper reefs, such as the East and West Flower Gardens off the coasts of Texas and Louisiana (Harry 1986*b*). In other areas, artificial hard-bottom seems to provide an attractive opportunity for *H. mcgintyi* settlement: according to Harry (1986*b*: 16), it 'is one of the most abundant oysters on offshore oil platforms, of which there are literally thousands in the waters, chiefly off Louisiana'. In sharp contrast, we are aware of but two reliable records of *H. hyotis* in the western Atlantic, both very recent and restricted to Florida: this present finding and another adult shell retrieved in 30 m depth off West Palm Beach in 2001 (G. Paulay, personal communication).

The exceptionally large size of *H. hyotis* implies that this species is unlikely to have been underrepresented in historical regional biotic surveys. Its discovery therefore most likely stems from a recent, previously undocumented invasion of the south-eastern USA coastline by Indo-Pacific taxa, as has lately occurred in the case of the black-lipped pearl oyster *Pinctada margaritifera* (Linnaeus, 1758) (Chesler 1994; Carlton 1996; M. Bukstel personal communication; R. D. Shearer personal communication) and more conspicuously the green mussel *Perna viridis* (Linnaeus, 1758) (via Trinidad; Benson *et al.* 2001; Ingrao *et al.* 2001). Transport via the international shipping industry, as part of fouling and/or bilge water fauna, has been implicated in these latter cases, and is likely involved in the case of *H. hyotis* as well.

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Ten new species of Mascarene land snails (Mollusca: Gastropoda) and their conservation status

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Abstract

Ten new species of Mascarene land snails are described from surveys carried out between 1990 and 2000 in the three islands of the Mascarenes. Eight of the species are endemic to Mauritius, one to Réunion and one to Rodrigues. While most of these species are assignable to genera already present in the archipelago, three of them belong to new genera. Apart from the Réunion species and one from Mauritius, which are critically endangered, all are known only as old shells from subfossil deposits and are presumed extinct. Some differences in diversity and extinction rates between the three islands are discussed.

Additional keywords: extinction rate, Mascarene Islands, Mauritius, Réunion, Rodrigues, subfossil, threatened species.

Introduction

Description of the terrestrial molluscs of the Mascarene islands (Réunion, Mauritius and Rodrigues) began as early as 1774 and to date 184 strictly terrestrial species are known, including 34 alien and three cryptogenic species (Griffiths and Florens unpublished data). Of the 147 known native species, 95% are endemic to the Mascarenes; however, endemism per island is somewhat lower given that many native species occur on more than one of the three islands. Thus island endemism reaches 63% for Mauritius, 57% for Rodrigues and 31.5% for Réunion (Griffiths and Florens unpublished data).

This paper describes ten new species of Mascarene snails and gives their conservation status according to IUCN criteria (IUCN 2001). Eight of these are apparently extinct species described from subfossil specimens from Mauritius and Rodrigues and two are extant species from Réunion and Mauritius.

All the species described here can be assigned to families occurring on the Mascarenes and continue to highlight the remarkable molluscan radiation of these isolated volcanic islands.

The higher classification used herein follows Beesley *et al.* (1998).

Materials and methods

The material described here was collected between 1990 and 2000 and comes from ~100 surveys totaling some 500 man-hours of sampling, mainly by Owen Griffiths (O. G.) and Vincent Florens (V. F.). Surveys were carried out on all three islands in a wide variety of habitats, ranging from the best preserved remnants of native forests to completely modified vegetation comprised solely of alien plant communities. Large ground species were visually searched for in the leaf litter, under rock overhangs and by overturning rocks and logs. Leaf litter samples were taken to sample microscopic species on the ground as well as in caves or under rock overhangs that contained some accumulation of soil or scree. Live arboreal species were surveyed by visual search of both foliage and tree trunks and by beating foliage above an inverted umbrella. Ecological notes, such as level of threats posed to the habitat by invasive alien species or degree of fragmentation of habitat, were taken at the sampling sites to allow an assessment of the threat categories of

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the species using the Categories and Criteria (version 3.1) of the IUCN Red List of Threatened Species (IUCN 2001). All type material has been lodged with the Australian Museum, Sydney (AMS).

Systematics

Superorder **CAENOGASTROPODA**

Order **ARCHITAENIOGLOSSA**

Superfamily **CYCLOPHOROIDEA**

Family **CYCLOPHORIDAE**

Subfamily **Cyclophorinae**

This subfamily occurs throughout the world except for the Americas. In the Mascarenes it is represented by three genera including those of the species described here.

Madgeaconcha n. gen.

Type species: *Madgeaconcha gerlachi* n. sp.

Diagnosis

Shell minute, height to width ratio ~1.6. Whorls 4.5, regularly increasing, convex. Suture impressed. Base rounded and smooth, umbilicus narrow and simple. Aperture circular with simple outer lip. Columella rounded or relatively straight, slightly reflected outwards over umbilicus. Parietal area thickened or undifferentiated. Protoconch smooth; teleoconch with faint growth lines and fainter striae visible under 40× magnification. Operculum corneous paucispiral. Radula taenioglossate; central teeth with dentate dorsal edge.

Remarks

This is a new genus, endemic to Mauritius and Réunion. Its main distinguishing features are the tiny, simple, conical shell, corneous paucispiral operculum and dentate dorsal edge of the central teeth of the radula. The exact taxonomic position of *Madgeaconcha* is not clear. Ponder (personal communication 2004) stated that 'the radula is reminiscent of cyclophorids although the central tooth is unusual, especially the top edge'. It may be a diplommatinid but there are no representatives of this family in the south-west Indian Ocean region. As the Mascarenes appear to have produced other aberrant cyclophorids, it is here placed in the Cyclophoridae. The type species was collected alive in Réunion at only one locality in an area of very humid native forest.

Etymology

Named for the late Dr E. H. Madge in honour of his work on Mascarene non-marine molluscs.

Madgeaconcha gerlachi n. sp.

(Figs 1, 2*E*, 3*B*)

Type material

Holotype. SE Réunion, 1 km west along Sentier Forestier du Tremblet along Ravine Pont Rouge, 55°47′48′′E 21°17′S, 300 m, in native forest with *Pandanus*, coll. J. Gerlach & O. G., 21 Jan. 1992 (AMS C204767).

Paratypes. Three adult and two juvenile shells from the type locality (AMS C204768).

Description

Shell minute, solid, elongate. Spire outline straight. Whorls ~4.5, including the protoconch, regularly increasing, very convex. No differentiation between the protoconch and the teleoconch. Suture simple, deeply impressed. Base narrow, rounded, smooth, umbilicus narrow and simple. Aperture circular, simple, not thickened with simple outer lip. Columella relatively straight, slightly reflected outwards over umbilicus. Parietal area slightly thickened. Protoconch smooth; teleoconch with sculpture of faint growth lines and even fainter spiral striae only visible under high magnification (40×).

Radula. Taenioglossate; central teeth with five lateral cusps and row of small ridges along dorsal margin. Lateral teeth with 4–5 cusps including one large cusp. Inner marginal teeth with 6–7 cusps; outer marginal teeth with six cusps (Fig. 1*C*,*D*).

Operculum. Pale yellow, paucispiral with eccentric nucleus; inner side with ridge towards base (Fig. 1*A*,*B*).

Dimensions of holotype

Height 1.62 mm; diameter 1.00 mm; aperture height 0.57 mm.

Remarks

This species is known from only one locality in Réunion where it still survives and occurs on the underside of dead lily fronds in the leaf litter. This locality is gradually being invaded and degraded by invasive alien plants. Thus, using the Categories and Criteria (version 3.1) of the IUCN Red List of Threatened Species (IUCN 2001), the species is critically endangered (CR B1a + biii).

Etymology

Named for its co-discoverer, Dr Justin Gerlach, Scientific Co-ordinator, The Nature Protection Trust of Seychelles.

Madgeaconcha sevathiani n. sp.

(Figs 2*D*, 3*C*)

Type material

Holotype. Mauritius, 900 m west of Quinze Cantons, Vacoas, 20°18′00′′S 57°27′30′′E, 340 m, dead adult buried in deposits at the base of cliff on upper scarps of Rivière du Rempart valley in nearly pure alien secondary vegetation, coll. Cláudia Baider & V. F., 11 Sep. 2000 (AMS C204769).

Paratype. One adult shell from the type locality (AMS C205039).

Description

Shell minute, solid and elongate, with spire outline slightly convex. Whorls ~4.5 regularly increasing, suture impressed. Base rounded and smooth, umbilicus simple and narrow. Aperture circular, thickened internally, with simple outer lip. Columella rounded, only slightly reflected over umbilicus. Parietal area undifferentiated. Protoconch smooth; teleoconch with sculpture of faint growth lines and fainter spiral striae visible under high magnification (40×).

Dimensions of holotype

Height 1.15 mm; diameter 0.70 mm; aperture height 0.37 mm.

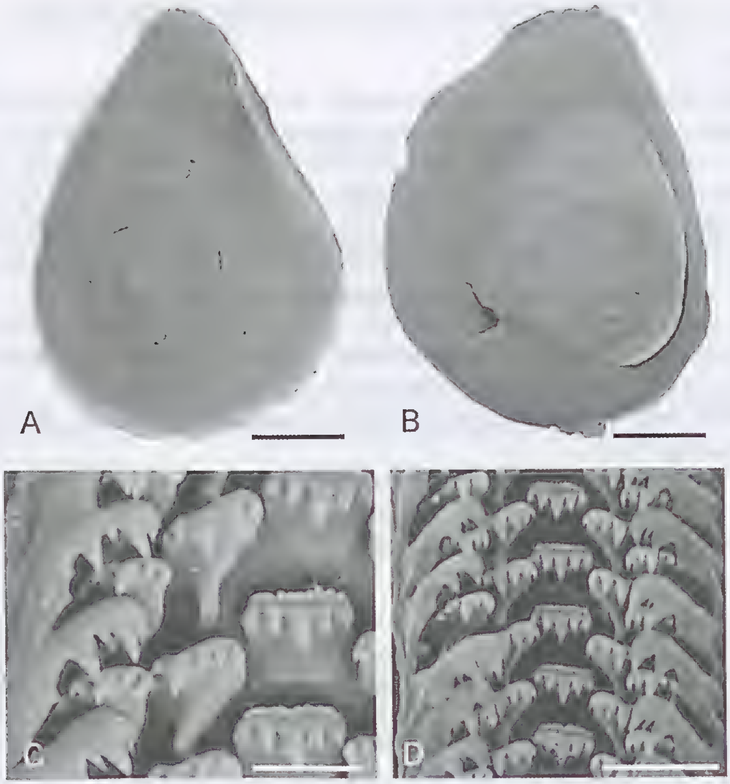

Fig. 1. *Madgeaconcha gerlachi* operculum, showing outer (*A*) and inner (*B*) sides. *Madgeaconcha gerlachi* radula showing half (*C*) and full (*D*) rows. (*A*,*B*) Scale bar = 150 µm; (*C*) scale bar = 5 µm; (*D*) scale bar = 10 µm.

Remarks

This species is the smallest snail yet found in the Mascarenes. It has a thicker shell and slightly less rounded whorl periphery than *M. gerlachi* n. sp. and the sutures are not as deeply impressed. It is 30% smaller in size. Despite considerable survey effort in a wide variety of habitats, it is only known from three old dead shells found deep in one subfossil deposit together with a large number of extinct endemic species. It is thus considered likely to be extinct.

Etymology

Named after Mr Jean-Claude Sevathian in recognition of his significant contribution to botany and native plant conservation in Mauritius.

Naggsiaconcha **n. gen.**

Type species: *Naggsiaconcha mauritianus* n. sp.

Diagnosis

Shell small, very elongate. Whorls ~11.5, regularly increasing, slightly convex. Suture deeply impressed, channeled. Base slightly angulated. Umbilicus very narrow, almost

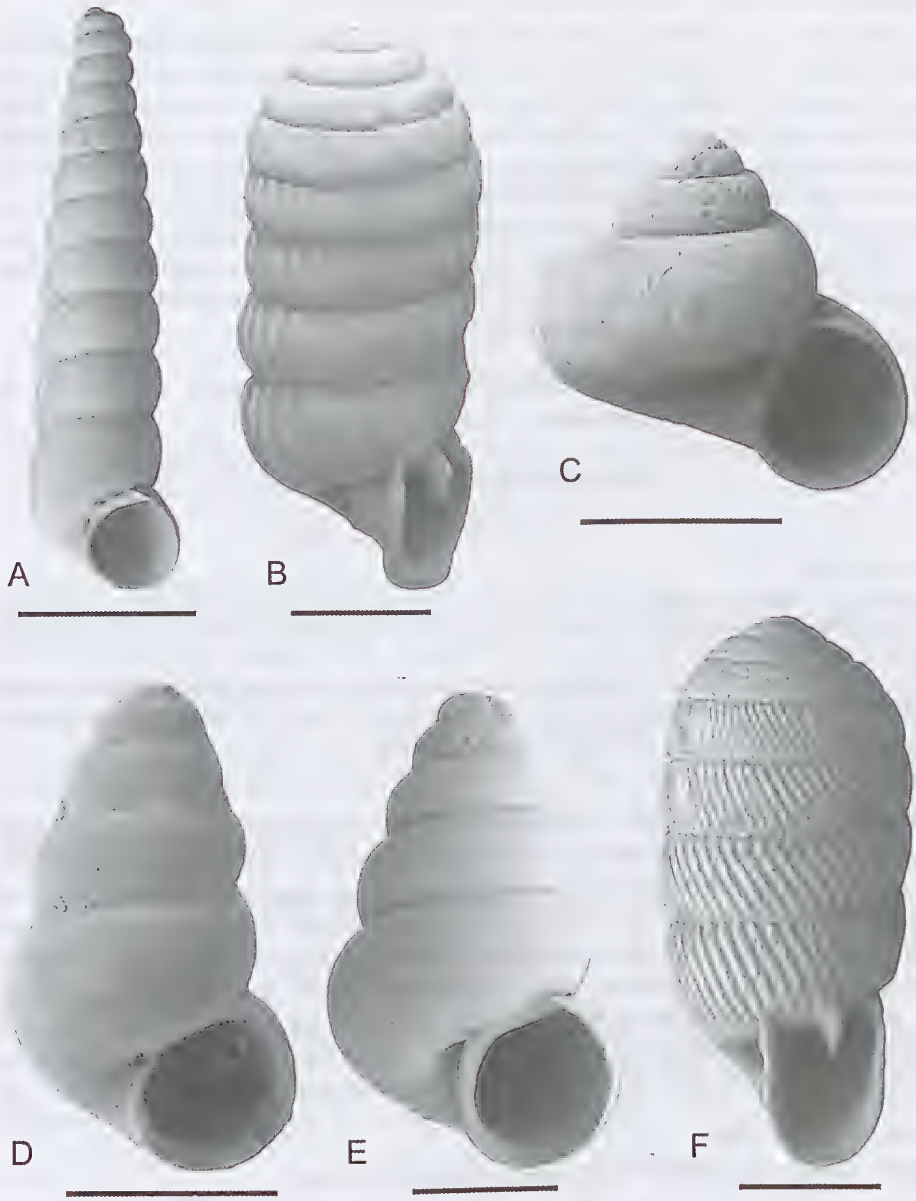

Fig. 2. (*A*) *Naggsiaconcha mauritianus* n. sp., holotype; (*B*) *Microstrophia baideri* n. sp., holotype; (*C*) *Omphalotropis bassinblancensis* n. sp., holotype; (*D*) *Madgeaconcha sevathiani* n. sp., holotype; (*E*) *Madgeaconcha gerlachi* n. sp., holotype; (*F*) *Microstrophia abnormala* n. sp., holotype. (*A–C*) Scale bar = 1 mm; (*D,E*) scale bar = 0.5 mm; (*F*) scale bar = 2 mm.

completely covered by the reflected columella. Aperture circular, simple. Outer lip simple. Protoconch ~1 whorl, malleated and bearing very faint radial lines. Teleoconch sculptured with fine irregular oblique radial ribs crossed by few very faint spiral lines.

Remarks

This new genus is endemic to Mauritius. Its main distinguishing features are its very elongate shell with a large number of whorls (11.5), circular aperture and tiny size. The exact taxonomic position of the type species has prompted some debate. Dr F. Naggs (BMNH (British Museum of Natural History, London), personal communication 1998) considered that it may be a subulinid or possibly a coellaxinid but subsequently rejected the latter. Ponder (personal communication 2000) considered the species as an aberrant cyclophorid based on the general shell form and circular aperture, which is followed here. This tiny species could not be placed in any known genus. The type specimen comes from a deposit dated at 2500–1000 years BP (Goodfriend, personal communication 1992).

Etymology

Named for Dr Fred Naggs of the Natural History Museum, London, for assisting the authors in their work over many years.

Naggsiaconcha mauritianus n. sp.
(Figs 2*A*, 3*A*)

Type material

Holotype. Mauritius, Snail Rock, 2 km S of Port Louis, 20°11′24′′S 57°30′40′′E, 400 m, dead adult buried in subfossil deposits under rock overhang, in degraded native forest, coll. O. G., Jun. 1990 (AMS C204760).

Paratypes. Four juvenile, two subadult and three adult shells from the type locality (AMS C204761); two adult shells, Mauritius, just below summit of Le Pouce Mt., 20°11′44′′S 57°31′20′′E, 650 m, from leaf litter in native forest, coll. O. G., 20 Jun. 1990 (AMS C204762).

Description

Shell small, thin, very elongate, spire outline straight. Protoconch ~1 whorl; teleoconch ~10.5 whorls, regularly increasing. Apical whorls more convex than subsequent whorls. Suture deeply impressed, channeled, slightly crenulated. Base slightly angulated, with angulation disappearing on last whorl. Umbilicus very narrow, almost completely covered by reflected columella. Aperture circular, simple, base sloping backwards with respect to vertical axis of shell (prosocline). Columella slanted, narrow, slightly reflected. Parietal area thickened, slightly raised from previous whorl. Outer lip simple, not reflected. Protoconch malleated and bearing very faint radial lines (Fig. 3*A*). Teleoconch sculptured with fine irregular oblique radial ribs crossed by few very faint spiral lines.

Dimensions of holotype

Height 3.55 mm; diameter 0.87 mm; aperture height 0.60 mm.

Remarks

Although no live individuals have been seen, this species possibly survives in remnants of native forests on Le Pouce Mountain near Port Louis where it has been collected dead in the leaf litter. Given that invasive alien weeds are currently degrading this forest, the species must be considered as critically endangered (CR B1a + biii) (IUCN 2001). Recent surveys at Bassin Blanc and Rivière du Rempart yielded additional subfossil specimens belonging to the same genus (V. Florens personal collection). Bassin Blanc specimens are two and a half times smaller and appear smoother; specimens from Rivière du Rempart are also smaller, and possess both peripheral and umbilical keels, which are absent on the presently described species. These possibly represent two additional species of *Naggsiaconcha*.

These will be described in a subsequent paper pending additional fieldwork to find more specimens in better condition.

Etymology

Named after Mauritius, the country of origin.

Superorder **CAENOGASTROPODA**

Order **SORBEOCONCHA**

Superfamily **RISSOOIDEA**

Family **ASSIMINEIDAE**

Subfamily **Omphalotropinae**

This subfamily is confined to Southeast Asia, the south-west Pacific and islands of the Indian Ocean. In the Mascarenes it is represented by two genera, *Omphaloptropis* (Germain 1921) and *Ditropisena* (Griffiths and Florens unpublished data).

Omphalotropis Pfeiffer, 1851

Type species: *Bulimus hieroglyphicus* Potiez & Michaud, 1838.

This genus, as currently recognised, has the same distribution as the subfamily. In the Mascarenes the genus comprises 20 species (Griffiths and Florens unpublished data), which are all Mascarene endemics, excluding those described below.

This genus of small terrestrial snails is characterised by having conical to elongate shells, with smooth to complex sculpture. Gills are greatly reduced and eyes are situated at the outer bases of relatively short tentacles. The operculum is corneous. The shell of the type species (from Mauritius) is small, thin, slender with tall spire and widely umbilicate. The whorls are weakly convex with a shallow suture (Fukuda and Ponder 2003).

Omphalotropis bassinblancensis n. sp.

(Figs 2*C*, 3*F*)

Type material

Holotype. Mauritius, 200 m south of Bassin Blanc crater lake, 20°27′10′′S 57°28′10′′E, 480 m, in remnants of native montane forest, dead adult buried in deposits under rock overhang at base of cliff in valley, coll. V. F., 3 Feb. 1998 (AMS C204765).

Paratypes. Two adult shells from the type locality (AMS C204766).

Description

Shell small, thin and low conical. Protoconch one whorl; teleoconch three whorls, regularly increasing, very convex. Last whorl comprising two thirds of shell, slightly detached from previous whorl. Suture on protoconch slightly impressed, becoming more impressed in subsequent whorls. Base very rounded. Umbilicus wide and deep. Aperture almost 'D' shaped. Columella simple, slanted, almost straight and slightly reflected. No differentiation between columella and parietal area. Outer lip simple. Protoconch and upper 2.5 teleoconch whorls faintly malleated; subsequent teleoconch whorls smooth except for faint irregular growth lines visible only under high magnification (40×).

Dimensions of holotype

Height 1.87 mm; diameter 1.85 mm; aperture height 0.84 mm.

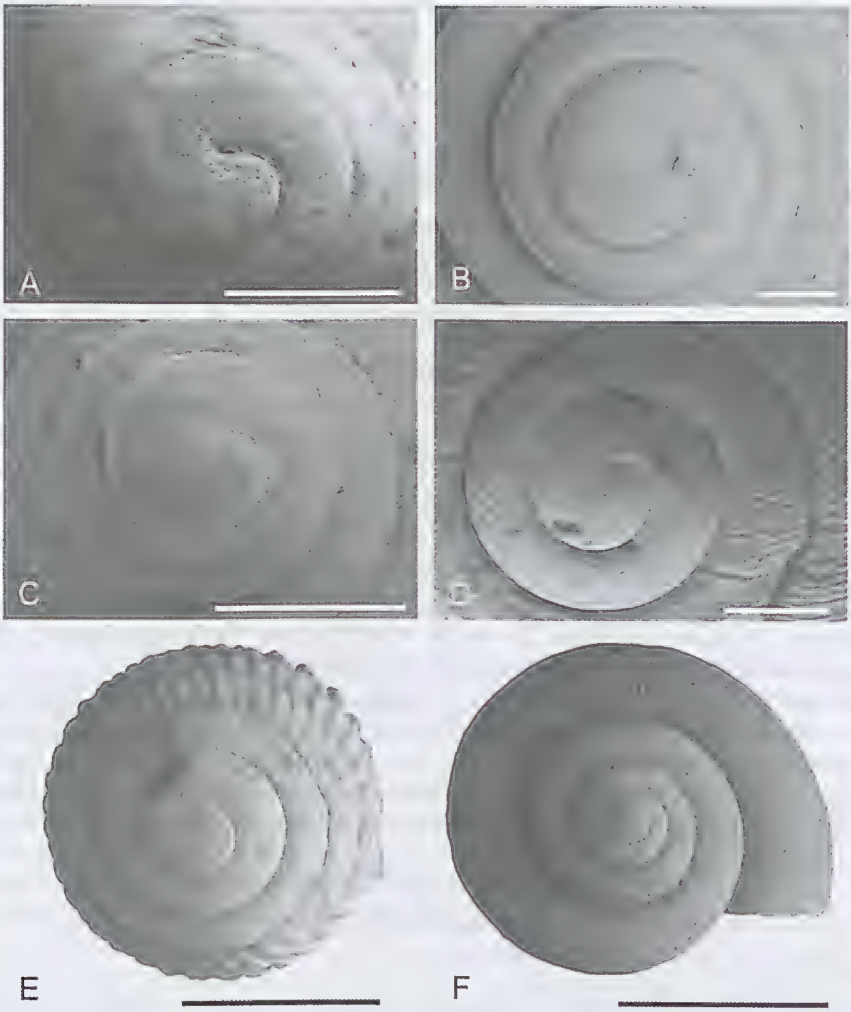

Fig. 3. (*A*) *Naggsiaconcha mauritianus* n. sp., protoconch, holotype; (*B*) *Madgeaconcha gerlachi* n. sp., protoconch, holotype; (*C*) *Madgeaconcha sevathiani* n. sp., protoconch, holotype; (*D*) *Microstrophia abnormala* n. sp., protoconch, holotype; (*E*) *Microstrophia baideri*, n. sp., protoconch, holotype; (*F*) *Omphalotropis bassinblancensis* n. sp., protoconch, holotype. (*A*,*C*) Scale bar = 0.2 mm; (*B*) scale bar = 0.1 mm; (*D*) scale bar = 0.5 mm; (*E*) scale bar = 1 mm; (*F*) scale bar = 1 mm.

Remarks

This species is the smallest of the genus in the Mascarenes. The only species of comparable size, albeit slightly larger, are *O. antelmei* Madge, 1946, *O. stevanovitchi* Griffiths, 2000 and *O. vacoasensis* n. sp., which differ from *O. bassinblancensis* in lacking the wide umbilicus as well as in having shells substantially higher than wide. Indeed *O. bassinblancensis* has a virtually equidimensional shell, a feature unique in Mascarene *Omphalotropis*. It is possible that this species belongs to a different genus but pending a comprehensive review and the eventual collection of better material we suggest its placement in *Omphalotropis*. Despite considerable survey efforts in its type locality and

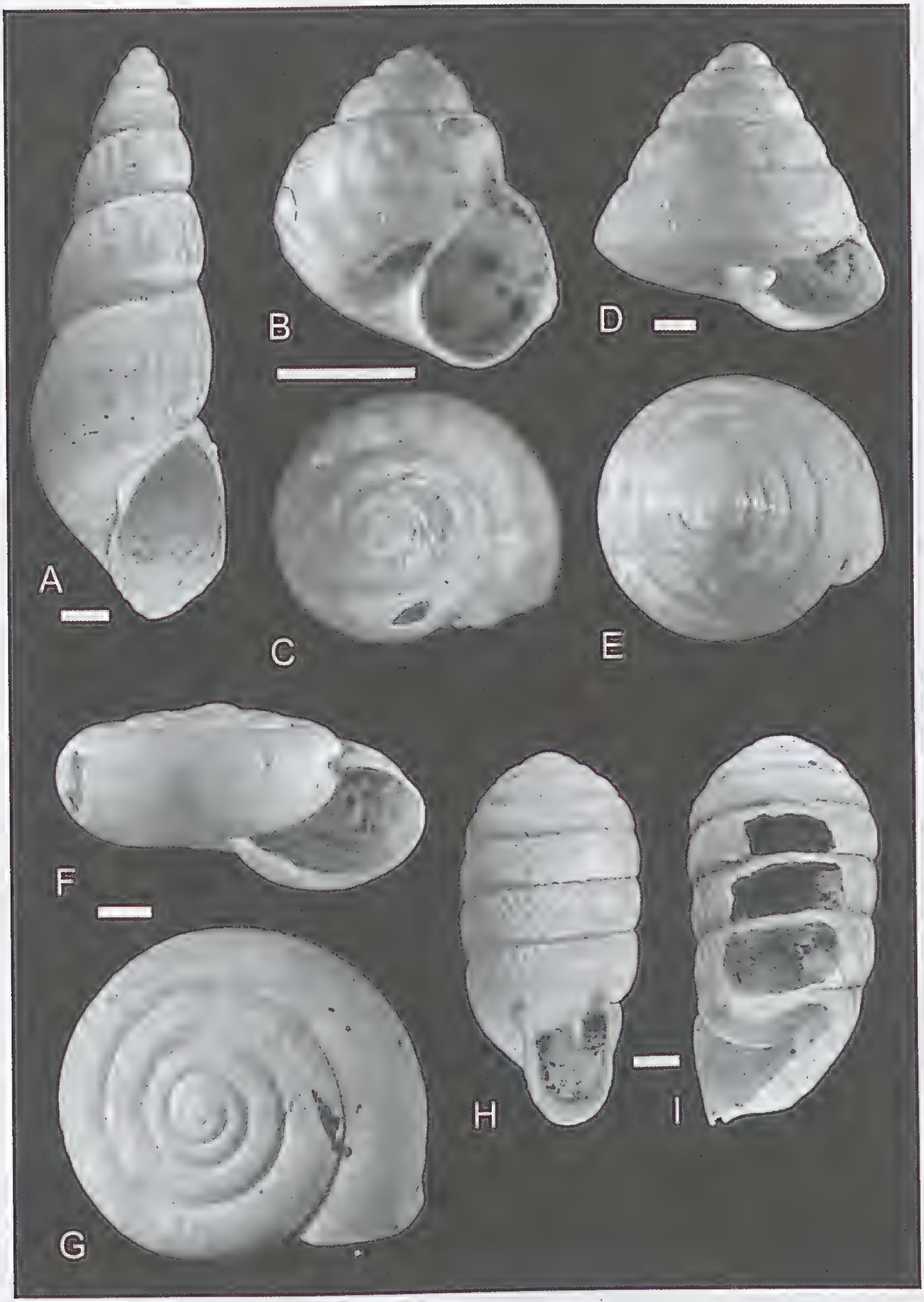

Fig. 4. (*A*) *Omphalotropis quittorensis* n. sp. holotype; (*B,C*) *Ompholotropis vacoasensis* n. sp., holotype; (*D,E*) *Erepta pyramidalis* n. sp., holotype; (*F,G*) *Erepta chloritiformis* n. sp., holotype; *H*, *Microstrophia abnormala* n. sp., holotype; (*I*) *Microstrophia abnormala* n. sp., paratype. (*A,B,D,H,I*) Scale bar = 1 mm; (*F*) scale bar = 2 mm.

elsewhere in Mauritius, only old dead specimens from subfossil deposits have been found. It is thus considered likely to be extinct.

Etymology

Named for its type locality.

Omphalotropis vacoasensis n. sp.

(Fig. 4*B,C*)

Type material

Holotype. Mauritius, 900 m west of Quinze Cantons, Vacoas, 20°18′00′′S 57°27′30′′E, 340 m, dead adult buried in deposits at the base of cliff on upper scarps of Rivière du Rempart valley in nearly pure alien secondary vegetation, coll. Cláudia Baider & V. F., 11 Sep. 2000 (AMS C204753).

Paratype. One adult shell from the type locality (AMS C204754).

Description

Shell small, thin and turbinate. Protoconch of one whorl; teleoconch three whorls, regularly increasing, convex and slightly shouldered; suture strongly impressed, slightly channeled. Base rounded. Umbilicus narrow, deep. Aperture ovate-lunate to pear shaped. Outer lip simple, not reflected. Columella slanted, slightly reflected outwards, partially closing umbilicus. Columella merges into parietal area. Protoconch smooth, teleoconch whorls with fine regular growth lines crossed by fine spiral lines above shoulder and coarser spiral ribs below; spiral rib around periphery of last whorl slightly more pronounced than others. Spiral ribs below periphery less pronounced. Shell with more or less radial streaks of brown most pronounced on last whorl.

Dimensions of holotype

Height 2.32 mm; diameter 2.11 mm; aperture height 1.24 mm.

Remarks

This species is readily distinguished from the three other known small Mascarene *Omphalotropis*, namely: *O. bassinblancensis* n. sp., *O. antelmei*, which lacks the distinctive sculpture of spiral ribs crossed by growth lines, and *O. stevanovitchi*, which, although having comparable sculpture, is relatively more elongate and lacks the striking radial brown streaks of *O. vacoasensis*. Despite considerable survey efforts over the whole island, it has only ever been found in the type locality, where two deeply buried old dead specimens have been uncovered from a subfossil deposit among several extinct endemic species. It is thus considered likely to be extinct.

Etymology

Named for the type locality.

'*Omphalotropis*' *quittorensis* n. sp.

(Fig. 4*A*)

Type material

Holotype. Rodrigues, Caverne Bambara, east side of Anse Quittor reserve just north of eastern end of airport runway, Plaine Corail, 19°45′22′′S 63°21′59′′E, 30 m, dead adult in limestone scree, coll. Carl G. Jones & O. G., Dec. 1997 (AMS C204755).

Paratypes. Four adult shells from the type locality (AMS C204756); six adult shells, Rodrigues, Caverne L'Affouche, east of Anse Quittor reserve, Plaine Corail, 19°45´24´´S 63°22´07´´E, 40 m, coll. Carl G. Jones & O. G., Dec. 1997 (AMS C204757).

Description

Shell fusiform, thick, elongate, spire outline straight to slightly convex. Protoconch 2.5 whorls; teleoconch ~7.5 whorls, convex, with slight sub-peripheral angulation, regularly increasing, but with each whorl descending below peripheral angle, producing deep, wide suture. Umbilical chink present, umbilical keel very faint. Aperture compressed, narrowly suboval, slightly pointed at upper extremity, pointed and flared at base. Outer lip thin, simple, not reflected. Columella strongly slanted, slightly reflected outwards, covering umbilicus in upper part. Parietal area narrow, undifferentiated. Protoconch faintly malleated and glossy, teleoconch with more eroded appearance and bearing very faint irregular growth lines crossed by less faint spiral lines visible only under 25× magnification. Last four whorls bearing orange-brown radial streaks separated by white bands.

Dimensions of holotype

Height 12.36 mm; diameter 4.15 mm; aperture height 4.04 mm.

Remarks

The exact taxonomic position of this species is not certain. Dr F. Naggs (BMNH, personal communication 1998) suggested that it could be a peculiar subulinid but its heavy shell, continuous peristome and slight sub-peripheral angulation with markedly grooved sutures lead him to conclude that it is a 'prosobranch', possibly an unknown thiarid. The markedly grooved suture is consistent on most shells examined. Ponder (AMS, personal communication 2000) considered this to be an *Omphalotropis* 'in the broad sense'. The subfossil deposits that yielded this species are exclusively terrestrial. Furthermore the Mascarenes have produced very elongate *Omphalotropis*. Thus Ponder's suggestion is followed here.

This species attains the greatest height among all the Mascarene members of the genus. Only two Mascarene *Omphalotropis* species, *O. clavula* (Morelet, 1866) and *O. hieroglyphica* (Potiez & Michaud, 1838), share the elongate shape of *O. quittorensis*. Both are, however, substantially smaller reaching at most three quarters of the latter's height. Further differences are the notching of the anterior end of the aperture by the umbilical keel in *O. hieroglyphica* and the presence of radial ribs in the last whorls in *O. clavula*. Despite considerable survey effort in Rodrigues, only old dead specimens have ever been collected in subfossil deposits. It is thus considered likely to be extinct.

Etymology

Named for the type locality.

Order **STYLOMMATOPHORA**

Superfamily **HELICARIONOIDEA**

Family **HELICARIONIDAE**

Subfamily **Ereptinae**

This subfamily is endemic to the Mascarenes and Madagascar, where it is represented by nine genera.

Erepta Albers, 1850

Type species: *Helix stylodon* Pfeiffer, 1842.

This genus is endemic to Mauritius and Réunion, where there are five species (Griffiths 2000) in addition to those described below. It is characterised by small to medium-sized, depressed to conic shaped shells, all having a distinct callus on the inner peristome near the umbilicus.

Erepta chloritiformis n. sp.

(Fig. 4F,G)

Type material

Holotype. Mauritius, 900 m west of Quinze Cantons, Vacoas, 20°18′00′′S 57°27′30′′E, 340 m, dead adult buried in deposits at the base of upper scarps of Rivière du Rempart valley in nearly pure alien secondary vegetation, coll. Cláudia Baider & V. F., 11 Sep. 2000 (AMS C204750).

Paratypes. Two juvenile shells from the type locality (AMS C204751).

Description

Shell thin, depressed, almost planispiral, glossy, pale brown above, off-white below. Protoconch, white, ~1 whorl, not clearly differentiated from the teleoconch. Teleoconch whorls four, regularly increasing, convex. Suture deeply impressed, channeled. Umbilicus wide, deep, cavernous, diameter ~14% of shell diameter. Aperture lunate, slightly depressed. Outer lip thin, slightly reflected, sinuous at base. Columella thickened and reflected outwards. Distinct callus on inner peristome near umbilicus. Parietal area slightly thickened, glazed. Protoconch almost smooth, with very faint spiral lines. Teleoconch with fine closely spaced oblique radial lines cut by fine spiral lines giving shell, particularly spire, decussate appearance under magnification. Base flattened, bearing prominent irregular ridges radiating from umbilicus and gradually attenuating into radial lines towards periphery where slight decussate sculpture discernible.

Dimensions of holotype

Height 6.92 mm; diameter 14.05 mm; aperture height 5.60 mm; umbilicus width 2 mm.

Remarks

This species possesses the characteristic columellar callus and protoconch spiral sculpture of *Erepta*. Of the seven species comprising this genus, *E. chloritiformis* has the most depressed shell of all, being over two times as broad as high. Its broad umbilicus also differentiates it from *E. odontina* (Morelet, 1851), *E. stylodon* (Pfeiffer, 1842), *E. pyramidalis* n. sp. and *E. wendystrahmi* Griffiths, 2000. While the two remaining *Erepta*, namely *E. thiriouxi* (Germain, 1918) and *E. setiliris* (Benson, 1859), both have an umbilicus, neither has the decussate sculpture of *E. chloritiformis*. Furthermore, *E. thiriouxi* lacks the rounded periphery of *E. chloritiformis* and is 30% smaller in diameter while *E. setiliris* possesses prominent radial ridges on the upper side of the shell, which are absent in *E. chloritiformis*, and is about half the diameter of the latter. Despite considerable survey effort, this distinctive snail has only been found as old shells in a subfossil deposit at the type locality. An old shell fragment comprising the umbilical region (V. Florens personal collection) found in a subfossil deposit in a lava pit south of Mont Blanc may also belong to this species. The species is thus considered likely to be extinct.

Etymology

Named for the striking resemblance of this species to members of the camaenid genus *Chloritis*.

Erepta pyramidalis n. sp.

(Fig. 4*D,E*)

Type material

Holotype. Mauritius, 750 m S. of Mont Blanc, 20°28′35′′S 57°29′15′′E, 190 m, dead adult buried in deposits under rock overhang on upper scarps of lava pit, in nearly pure alien secondary vegetation, coll. V. F, 1 Nov. 1997 (AMS C204752).

Description

Shell solid, trochoidal conical and pale brown. Spire outline straight to slightly convex. Protoconch whorls 1.5. Teleoconch whorls ~4.75, slightly convex, regularly increasing, suture weakly impressed, last whorl with strongly angulated periphery. Base flat, umbilicus closed. Aperture compressed-lunate, lip thickened on inside. Columella strongly reflected outwards. Pronounced tooth-like callosity on inner side of peristome. Region where columella joins base of whorl broadly excavated. Parietal area indistinct. Protoconch with fine spiral lines; teleoconch with fine radial growth lines crossed by spiral ribs, giving shell decussate appearance under 40× magnification. Underside of shell bearing similar decussate sculpture, particularly near periphery.

Dimensions of holotype

Height 6.95 mm; diameter 6.95 mm; aperture height 2.29 mm; aperture width 2.78 mm.

Remarks

This species possesses the characteristic columellar callus and protoconch spiral sculpture of *Erepta*. It is readily distinguishable from all other species of *Erepta* in possessing a strong keel and a high spire that gives it its pyramidal shape. It is consequently equidimensional, a feature hitherto not observed in the genus and in stark contrast with the depressed shells of its sister species. Even though only one specimen was found, we believe it warrants species status given its strikingly distinguishing features. Several other species were represented at the same site by only one or two shells and no species of *Erepta* occurred there in numbers. Despite considerable survey efforts no living material or fresh shells could be found of this species and it is thus considered likely to be extinct.

Etymology

Named for its pyramidal shape that is unique for the genus.

Superfamily **STREPTAXOIDEA**

Family **STREPTAXIDAE**

This family has an Afro-Oriental-Neotropical distribution. In the Mascarenes there are seven native genera and one cryptogenic genus (Griffiths and Florens unpublished data). The extensive radiation of Streptaxidae in the Mascarenes is one of the major features of the fauna, with 41 native and one cryptogenic species already described (Griffiths and Florens unpublished data).

Microstrophia Mollendorf, 1887

Type species: *Pupa clavulata* Lamarck, 1822.

This genus occurs only on Mauritius, where it is represented by four species (Griffiths 2000) in addition to those described below. *Microstrophia* is considered by some authors (Zilch 1959) to be a subgenus of *Gonospira*. It is considered as a full genus here following Schileyko (2000). It is characterised by small elongate shells with narrow apertures containing strong apertural lamella and juvenile shells having a very wide umbilicus.

Microstrophia abnormala n. sp.

(Figs 2*F*, 3*D*, 4*H*,*I*)

Type material

Holotype. Mauritius, 900 m west of Quinze Cantons, Vacoas, 20°18′00′′S 57°27′30′′E, 340 m, dead adult buried in deposits at the base of cliff on upper scarps of Rivière du Rempart valley in nearly pure alien secondary vegetation, coll. Cláudia Baider & V. F., 11 Sep. 2000 (AMS C204758).

Paratypes. Four adult and subadult shells from the type locality (AMS C204759).

Description

Shell pupiform, white. Protoconch one whorl; teleoconch ~7.25 whorls, last half whorl slightly constricted at base. Suture shallow, crenulated. Base tapering. Umbilicus deep and slit like. Aperture narrowly ovate-lunate with three barriers: one strong parietal lamella extending from half-whorl deep inside aperture to plane of outer lip where it slants slightly to right; small low basal barrier commencing inside aperture at middle palatal level and extending short way further in; strong columellar plait deep inside aperture formed by internal projection of slit-like umbilicus. Outer lip thickened, reflected outwards with shallow constriction mid-way down. Columella thickened, slightly reflected outwards, almost straight. Parietal area broad and glazed. Protoconch with faint irregular radial lines imparting malleated appearance; teleoconch covered in strong oblique radial ribs perceptibly stronger at each succeeding whorl. Troughs between radial ribs spirally striate on either side of sutures, particularly on lower side, except on last whorl where spiral striae also occur further from suture.

Dimensions of holotype

Height 7.92 mm; diameter 3.88 mm; aperture height 2.26 mm.

Remarks

Young juveniles have a broad umbilicus that narrows progressively as the shell grows. This feature, together with the strong radial ribs and strong parietal lamella, justify placing this species in *Microstrophia*. It also shares the spiral striae present in other members of *Microstrophia* with the exception of *M. nana* Peile, 1936. Although it superficially most resembles *M. clavulata* (Lamarck, 1822), this species differs from the latter and all other *Microstrophia,* in several important ways, including possession of: (*1*) a parietal lamella that extends very deeply into the aperture; (*2*) a low blunt ridge seated deeply in the aperture in the middle palatal region; (*3*) a strong columellar plait resulting from a slight kink in the last half whorl; (*4*) radial ribs set more obliquely, reminiscent of *Gonospira*; and (*5*) a relatively wide aperture again more reminiscent of *Gonospira*. It is thus a species combining certain features of *Microstrophia* and *Gonospira* while also possessing unique features absent from these two genera. Subadults possess a roughly t-shaped aperture as a

result of the deep apertural ridges described above. Apart from the type locality, this species was also found at Bassin Blanc, in the south of Mont Blanc, and on Ile aux Aigrettes (V. Florens personal collection) together with shells that have been dated at 15000–5000 years BP (Goodfriend, personal communication 1992). Despite considerable survey effort this species has not been found other than in subfossil deposits and is thus considered likely to be extinct.

Etymology

Named for the possession of features hitherto unrecorded in *Microstrophia*.

Microstrophia baideri n. sp.

(Figs 2*B*, 3*E*)

Type material

Holotype. Mauritius, 900 m west of Quinze Cantons, Vacoas, 20°18′00′′S 57°27′30′′E, 340 m, dead adult buried in deposits at the base of cliff on upper scarps of Rivière du Rempart valley in nearly pure alien secondary vegetation, coll. Cláudia Baider & V. F., 11 Sep. 2000 (AMS C204763).

Paratypes. Two adult and one juvenile shell from the type locality (AMS C204764).

Description

Shell white, cylindrical-pupiform, spire outline straight except first four strongly domed whorls. Protoconch: one whorl, flat, smooth; teleoconch: seven whorls, regularly increasing, slightly convex. Suture shallow, crenulate. Base tapered. Umbilicus closed in adults, very narrow, almost circular in juveniles. Aperture elongate, compressed vertically, set distinctly to right of vertical axis of shell. Aperture edge thickened, reflected. A strong slightly sinuous parietal lamella extends one third of aperture length into aperture. Upper right part of aperture recessed back, forming sinus-like slit to right of parietal lamella. Columella thickened, reflected, almost straight. Parietal area thickened and raised forming continuous edge to left of parietal lamella. Teleoconch covered with regular, thick, prominent, radial ribs.

Dimensions of holotype

Height 4.22 mm; diameter 1.8 mm; aperture height 1.06 mm.

Remarks

This species possesses the type of sculpture and aperture characterising *Microstrophia*. However it is unique in that juvenile shells lack the broad umbilicus characteristic of all other species included in this genus. Its cylindrical shape and strong radial ribs are reminiscent of some *Cerion* species from Bahamas and distinguish it readily from the other five *Microstrophia* that possess relatively less strong ribs and various shapes different from the present. *M. baideri* is also the most elongate of the taxa included in *Microstrophia*, with a height to diameter ratio exceeding 2.3, as opposed to the other species that ranged from 1.65 to 2.0. This snail has only been found as shells in subfossil deposits at the type locality and at Bassin Blanc. Despite considerable survey efforts in these localities and elsewhere, no live or fresh specimens have been found and it is thus considered likely to be extinct.

Etymology

Named for Dr Cláudia Baider who co-discovered this species and several others.

Discussion

The fact that new taxa recently described from Mauritius and Rodrigues are overwhelmingly subfossil while new taxa from Réunion tend to be extant (Griffiths 2000; this study) seems to reflect the different degrees of deforestation between the three islands: original forested areas cover only ~5% of Mauritius (Safford 1997), < 1% of Rodrigues (Cheke 1987) and 30% of Réunion (Strasberg 1994). Consequently while just over a third of the native snail species of Mauritius and Rodrigues have already become extinct, only 12% of those from Réunion have disappeared (Florens and Griffiths 2000).

A feature of the Mascarenes that allows an understanding of their extinct snail fauna is the wealth of subfossil sites that occur there. These include limited limestone sites on Mauritius and Rodrigues, and large numbers of subfossil sites under large basalt boulders on all three islands. It is true to say that any collection of large basalt boulders in the Mascarenes, providing they have relatively dry overhangs and are orientated so as not to be scoured out by cyclonic rains, will yield subfossil snails ranging in age from the time of local forest clearance (approximately 200 years ago) to at least as old as sites such as at Snail Rock, south of the capital Port Louis, that have been dated at 2500–1000 years BP (Goodfriend, personal communication 1992). Such sites, while mostly yielding only snails, have on occasion yielded subfossil remains of other extinct fauna (Cowles 1987; Florens 2002).

These subfossil deposits continue to yield new snail species at a surprising rate. At least 19 new species were found between 1989 and 2000, representing a 13% addition to the hitherto known native terrestrial molluscs of the region. One trend in the discovery of these new species is that most come from the island of Mauritius. Fifteen (79%) of these new species occur on Mauritius as against three for Réunion and two for Rodrigues (the total exceeds 19 since one of the species occurs on two islands). Even accounting for the fact that Mauritius has a more diverse molluscan fauna, this trend in new species discoveries does seem to reflect the fact that the authors, who live on Mauritius, survey it far more extensively than the islands of Rodrigues and Réunion. It is thus probable that several new species await discovery once greater survey effort is made on these two latter islands, particularly on Réunion, which is larger and more diverse in habitat types.

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Short Contribution

Sexually dimorphic radular morphology in *Euplica varians* and *E. versicolor* (Neogastropoda: Columbellidae)

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Abstract

Radular morphology in two species of *Euplica* (Gastropoda: Neogastropoda: Columbellidae) was investigated for the occurrence of sexual dimorphism. Sexual dimorphism was found to occur in these columbellid species, as it does in some species of muricids, with adult males having tooth modifications including differences in cusp shape, larger tooth size in one species and more tooth rows in both. The functional significance of the dimorphism is unknown.

Additional keywords: Gastropoda, Mollusca, ontogeny, sexual dimorphism.

Introduction

The morphology of the radula, the chitinous strip of teeth found in molluscs, has traditionally been one of the most commonly used sources of data for studies on molluscan systematics. The shape and form of molluscan radular teeth are typically unique to a species or genus, and some features of the radula, such as tooth numbers, have been used to investigate higher level molluscan taxonomic relationships. Thus intraspecific variations in radular characteristics are important and must be documented if molluscan relationships are to be reconstructed rigorously.

Sexual dimorphism in radular morphology is known in one member of a basal gastropod group, the trochoidean species *Tricolia variabilis* (Robertson 1971). It is more common in caenogastropods and has been documented in muricid gastropods by Arakawa (1957) and Maes (1966), who studied species of *Drupella* and *Nassa* respectively. In both cases, variation was present primarily in the size and shape of the rachidian teeth, and *Drupella* also showed variation in aspects of lateral tooth size. Fujioka (1982) later investigated four species of *Drupella* in greater detail and found that the sexual dimorphism in radular tooth shape was not present in the juveniles, which had tooth shapes similar to adult females; change in tooth shape only occurred in the adult males. Fujioka (1984) studied the radulae of *Cronia margariticola* and *Morula musiva*, also muricids, and found sexual dimorphism to occur in the larger size and simpler shape of the rachidian teeth in adult males, similar to the situation in *Drupella*. Fujioka (1984) suggested that this may be linked to a difference in diet between the adult males and females. One buccinid species, *Pisania luctuosa*, was shown by Cernohorsky (1971) to exhibit sexual dimorphism in radular tooth row numbers, wherein males have fewer tooth rows and a wider radula.

The purpose of this paper is to describe dimorphic radulae present in *Euplica varians* and related species of columbellid gastropods. Columbellids are a diverse family of buccinoid neogastropods. Although they are mostly opportunistic carnivores, some members of the family, including species in the genus *Euplica*, are facultative herbivores. Radular morphology is one of the preferred character sets for investigating columbellid

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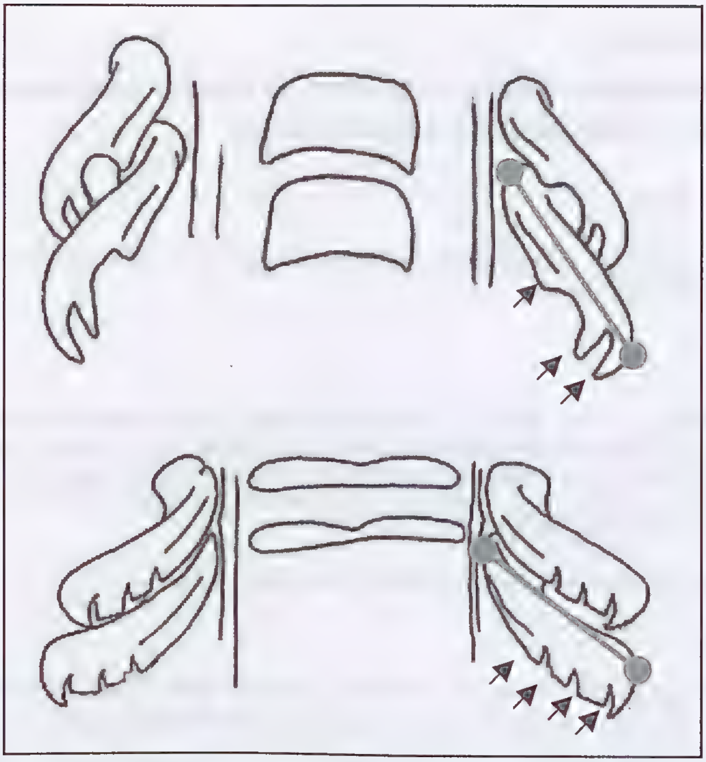

Fig. 1. Drawings of two rows each from a *Mitrella* radula (top) and that of *Euplica* (bottom). The double-ended lines on each indicate the main axis of the primary lateral tooth cusp, along which tooth length was measured. The arrows indicate the secondary (posterior) lateral cusps in each.

systematics at the generic level (Radwin 1977; Bhatti 1992) because it varies little within columbellid species or between closely related species, whereas shell morphology is often highly variable.

The columbellid radula is stenoglossate, but with an acuspate centre plate rather than a typical rachidian (Guralnick and deMaintenon 1997), and tall, sigmoid lateral teeth that rotate obliquely on narrow bases. Each lateral tooth has one primary cusp, with three to four secondary cusps along the posterior edge (Fig. 1 shows a typical columbellid radula compared with the radula of *Euplica*). Tooth wear patterns suggest that the lateral teeth contact the substrate obliquely along the posterior edge, most strongly at the end. Because radular morphology is conserved within columbellid species groups, intraspecific dimorphism in radular morphology may be both interesting from a functional perspective, and it may in itself be systematically informative.

Euplica, the focus of this study, is a group of about nine Indo-Pacific columbellid species, 5–25 mm in shell length, found commonly in shallow rocky or seagrass habitats. Radular morphology is similar in all members of the genus. The end-most (distal) secondary cusp is flat or pointed, the two medial secondary cusps are flat-edged and the proximal secondary cusp is blade-like, giving the posterior edge of the tooth a scraper-like form (Fig. 1, bottom). This state is characteristic of many columbellid species with a

partially herbivorous diet, whereas carnivores (Fig. 1, top) will typically have pointed secondary cusps with large spaces between them (deMaintenon 1999).

Materials and methods

Specimens of *Euplica varians*, a small widespread species, were collected from sites in the Hawaiian Islands and preserved in 70–90% ethanol. Specimens of *Euplica versicolor* (Sowerby, 1832), a larger species of *Euplica* native to the south-west Pacific, were available from collections made in New Caledonia. Sex, shell length and stage (juvenile or adult) were recorded for each specimen. Columbellids have determinate growth; the shell in a growing individual has a thin, fragile aperture edge, which becomes thickened and denticulate when the growth period is terminated. Thin-lipped individuals were recorded as juveniles, individuals with a thickened denticulate labial edge were recorded as adults. Because of this, recognition of adults in this study is likely to be conservative. Sex was determined by the presence of secondary sexual characteristics, including a penis in males or reproductive glands in females (the male pallial gonoduct is non-glandular).

Each specimen was dissected and the radula removed. Tooth rows were counted and the total number recorded, and radular tooth measurements made using an Olympus compound microscope with an ocular micrometer (Olympus, Melville, NY, USA). Two sample *t*-tests were used to investigate differences in mean radular measurements between adult males and females, and simple linear correlations were used to investigate ontogenetic changes in radular measurements as indicated by increasing shell size. For illustration, radulae from several individuals were mounted on stubs with double-stick conductive tape, and the radulae were sputter coated and viewed using an ISI electron microscope (Topcon America Corporation, Paramus, NJ, USA).

Results and discussion

Hawaiian *Euplica varians* has a maximum shell length of ~10 mm, and individuals cease growth and develop a thickened lip at 8.5–9.0 mm shell length or larger. Secondary sexual characteristics (and perhaps sexual maturity) appear before growth is completed, at ~7 mm shell length.

Radular morphology in *E. varians* is sexually dimorphic, but shape only differs in adults. Adult male and female *E. varians* differ in the shape of the outermost secondary lateral tooth cusp. Adult males have a pointed outermost cusp that extends past the posterior edge of the rest of the tooth (Fig. 2*a*), whereas subadult males and females have flat-tipped outer cusps with only a very slight point, giving the distal cusp a notched appearance (Fig. 2*b*). Two transitional specimens (both adults) were found with a longer distal cusp and a very small point at its base (the male in Fig. 2*a* is one of these), suggesting that the shift in radular form occurs after growth ceases. The specimens observed all had similar teeth from one end of the radula to the other (not counting wear), so no transitions were observed within individual radulae.

The width of the centre plates, lengths of the lateral teeth, and the number of tooth rows were recorded in each specimen of *E. varians* and compared relative to shell length to investigate ontogenetic trends (Fig. 3). The lateral tooth length and number of tooth rows both increase linearly with increasing shell length (Pearson's correlation coefficient and P-value given in Fig. 3), and those trends do not show any definitive quantitative change associated with cessation in growth or with sexual maturity. Radulae of adult males and females differ in one aspect of size; adult males have more tooth rows than adult females (t-test, $P = 0.008$, see Table 1 for means), though adult shell size and tooth length do not differ significantly.

Several adult specimens of *Euplica versicolor* were available from New Caledonia, and radular morphology was examined in eight of these. Because all available specimens were adults, no ontogenetic changes could be observed. The radula in this species differs from that of *E. varians* primarily in size; the basic tooth morphology is the same. The divergent

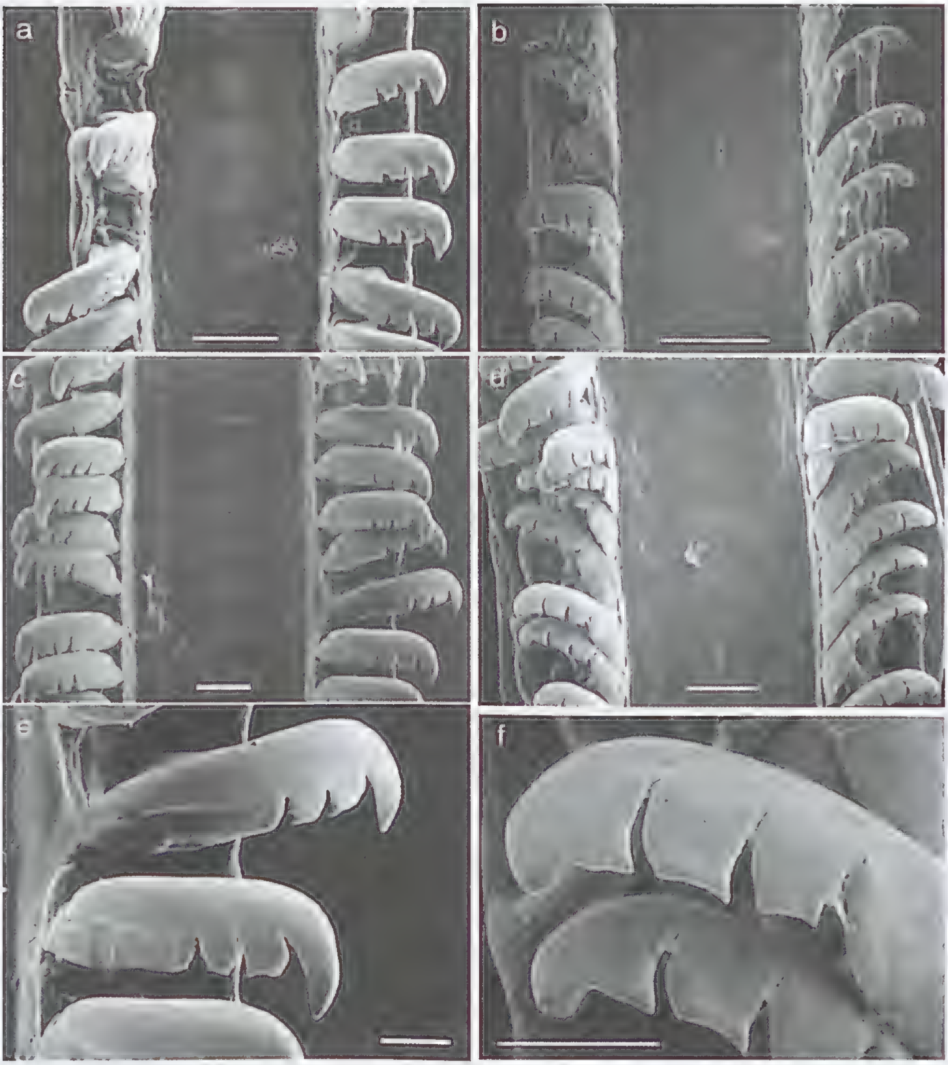

Fig. 2. (*a*) *Euplica varians* radula, adult male, 9.30 mm shell length, scale bar = 100μm. (*b*) *Euplica varians* radula, adult female, 8.40 mm shell length, scale bar = 100μm. (*c*) *Euplica versicolor* radula, adult male, 16.75 mm shell length, scale bar = 100μm. (*d*) *Euplica versicolor* radula, adult female, 17.90 mm shell length, scale bar = 100μm. (*e*) Lateral teeth, close-up of (*c*), scale bar = 50μm. (*f*) Lateral teeth, close-up of (*d*), scale bar = 50μm.

morphology found in *Euplica varians* was present in this species, with all four males having a pointed distal lateral cusp (Fig. 2*c,e*) and the females having a flatter distal secondary cusp (Fig. 2*d,f*). Lateral tooth length and number of tooth rows are also higher in males than in females (*t*-test, $P = 0.007$ and $P = 0.002$, respectively, see Table 2 for means) even though shell lengths are similar, but the available sample size was rather small.

The sexual dimorphism in the columbellid radulae appears to take the same form as seen previously in muricids: a variation in tooth cusp shape and size that only appears in adults. The buccinid *Pisania* may be similar, but female *Pisania* have more tooth rows than males

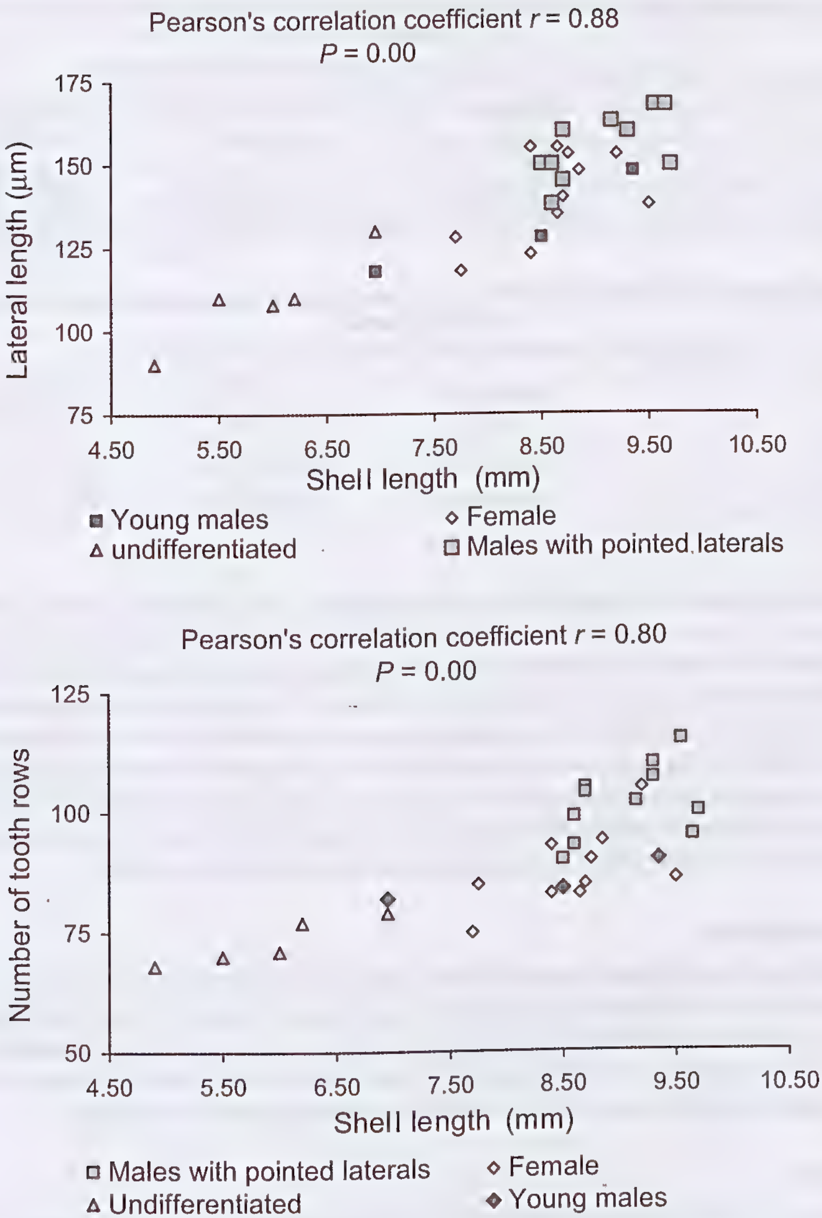

Fig. 3. (*a*) Scatter plot of shell length *v.* lateral tooth length for specimens of *Euplica varians* showing Pearson's correlation coefficient and probability. (*b*) Scatter plot of shell length *v.* number of tooth rows for specimens of *Euplica varians* showing Pearson's correlation coefficient and probability.

(Cernohorsky 1971), whereas female *Euplica* have less. The function of the dimorphism is unknown in both cases. Robertson (1971) suggested that it may be linked to dietary differences, but that possibility has not been investigated in these taxa. The presence of a similar characteristic evolving sporadically in members of four different families suggests that radular dimorphism might have some particular function.

Table 1. Means and standard errors for tooth measurements from male and female *Euplica varians* radulae

Asterisks indicate measurements that differed significantly between sexes

	n	Shell length (mm)	Lateral tooth length (µm)	Number of tooth rows*
Males	11	9.07 ± 0.14	155.64 ± 2.92	101.8 ± 2.3
Females	8	8.84 ± 0.12	147.13 ± 2.91	90.9 ± 2.8

Table 2. Means and standard errors for tooth measurements from male and female *Euplica versicolor* radulae

Asterisks indicate measurements that differed significantly between sexes

	n	Shell length (mm)	Lateral tooth length (µm)*	Number of tooth rows*
Males	4	16.65 ± 0.84	261.25 ± 7.18	140.0 ± 4.4
Females	4	16.14 ± 0.50	225.13 ± 5.40	112.3 ± 2.8

Sexual dimorphism in columbellids was investigated in two congeneric species, *Euplica varians* and *E. versicolor* in the present study. These species' radulae have rarely been illustrated. Sleurs (1985) figured the radula of *E. varians* and deMaintenon (1999) figured the radula of *Euplica bidentata*, a species very similar to *E. versicolor*; the latter was taken from an adult male and its tooth morphology is consistent with that. Sleurs (1985) appeared to have a female or young male. Radulae of other *Euplica* species and of members of the genus *Metanachis* are morphologically similar to the point of being indistinguishable, so the dimorphism may be present in these other species as well. In *E. varians*, the dimorphism has an ontogenetic basis and does not appear until the animal ceases growth.

Acknowledgments

I would like to thank Claude Berthault of the Paris Museum, Wes Thorsson on Oahu, and members of the NOWRAMP cruise to the north-west Hawaiian Islands (particularly Dwayne Minton and Mark Albins) for obtaining material, undergraduate volunteer Vince Montoya for helping with many hours of dissections, data collections and radular preparations, and John Coney for help with the scanning electron microscope.

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Short Contribution

Odour tracking to a food source by the gastropod *Meridolum gulosum* (Gould, 1864) from New South Wales, Australia (Camaenidae : Eupulmonata : Mollusca)

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Abstract

Some gastropods are able to find food sources by following airborne chemical plumes using both tropotaxis and anemotaxis. This study examined odour tracking to food odours with a species of terrestrial gastropod, *Meridolum gulosum* (Gould, 1864), a native to rainforests in coastal south-eastern New South Wales, Australia. It was demonstrated that *M. gulosum* moves towards food odours (fungus) in still air, and holds its tentacles at characteristic angles when moving towards an odour source. This snail can detect odours at least 12 cm away from the source in air.

Additional keywords: behaviour, chemoreception, Gastropoda, kinematics, orientation, snail, tentacle.

Introduction

Animals use cues from their environment to find mates and food. Gastropods sense many features about their environment and some can follow mucus trails and chemical odours in freshwater, marine and terrestrial systems (Chase *et al.* 1978; Chase 1986; Tankersley 1989; Levri 1998; Davies and Knowles 2001). Gastropods can track odours in air using both tropotaxis and anemotaxis (Chase and Croll 1981; Lemaire and Chase 1998). In this study, an Australian land snail from New South Wales was tested for odour tracking abilities and tentacle kinematics both when tracking and not tracking odours.

Understanding how gastropods track food odours and the speed at which they do so may assist in calculating dispersal rates of gastropods when moving to a new food source. This is important because many gastropods are narrow-range taxa and may live in threatened habitats (Ponder and Colgan 2002). No previous studies on odour tracking with gastropods have dealt with endemic Australian fauna, but studies have been carried out on the European garden snail *Cantareus aspersus* (Müller, 1774) (Farkas and Shorey 1976; Lemaire and Chase 1998), which occurs natively in Europe and is present also in parts of the USA and Australia. In addition, the natural history of the Australian rainforest snails of New South Wales is not well understood (Kay *et al.* 1998; Lemaire and Chase 1998; Puslednik 2002). This species, *Meridolum gulosum*, is endemic to the rainforest south of Sydney and has been shown previously to prefer fungus in a dietary preference study (Puslednik 2002).

Materials and methods

The gastropod *Meridolum gulosum* used in these experiments is a member of the Camaenidae. The specimens ($n = 3$) were collected on 25 February 2003 in the rainforest on Mt Kiera in Wollongong, New South Wales, Australia and the experiment was conducted within 24 h of collection. After the experiment, identification was confirmed by L. Puslednik and all specimens were returned to the rainforest.

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The food source chosen for this study was based on information from the literature. *Meridolum* spp. are fungivores and have been shown to readily consume commercial fungi, such as white button mushrooms (Solem 1998; Puslednik 2002); this habit also being suspected for many other camaenids (Solem 1998). *Meridolum gulosum* has not previously been shown to track odours.

All snails were kept in a group container for at least 4 h before being used in experiments. After being removed from the container, they were placed on plastic and sprinkled with water. They were only placed in the experimental arena after they began to crawl. Snails were not fed before experiments (8–24 h). Temperature ranged from 23 to 31°C with a mean of 25°C.

To test odour tracking abilities, an individual snail was placed at the centre of a square arena (25.4 cm long) that was divided into four equal quadrants with a cotton ball in each corner and allowed to crawl freely (Fig. 1). One of the four cotton balls was soaked in a solution of water and food to make an odour ball; the others were soaked in water alone. The surface of the testing arena was covered with clean plastic film (Saran Wrap, Indianapolis, IN, USA) for each trial, presenting each snail with a similar substrate and preventing any confounding orientation to pre-existing mucus trails. The orientation of the snail and odour ball placement were both chosen randomly. There was at least a 2-min break between trials to allow odours to dissipate.

The odour solution was a puree of the commercial fungus *Agaricus bisporus* (white button mushroom) and water. Trials were conducted indoors under artificial light, except for two trials conducted in the dark because those snails would not move in the lighted arena. Each snail was used only once. The air flow within

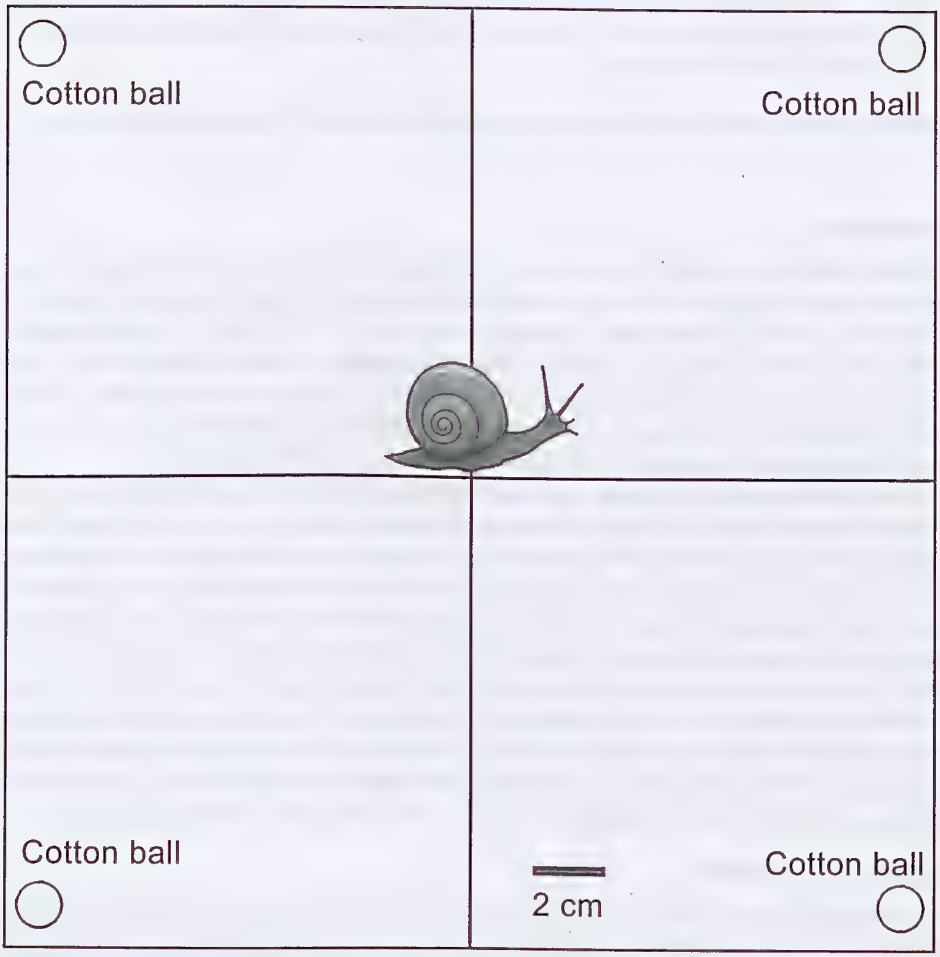

Fig. 1. Diagram of arena used to test odour tracking.

the room was relatively stationary and was not controlled. Trials were concluded when the snail exited the arena or reached a cotton ball. If a snail stopped moving for more than 20 min, its position was recorded and the trial was ended.

Trials were videotaped using a Sony PC101 camcorder (Sony, Tokyo, Japan) on Mini-Digital videotape. Observations on snails' behaviours were made during trials. The length and width of each specimen was measured before each trial. Snail shells ranged in size from 24 mm length × 27 mm width to 29 mm length × 33 mm width. The paths and tentacle positions were digitised using Motus digitising software (version 4; Peak Performance Technologies, Centennial, CO, USA). For the paths, three points were digitised: the most anterior part of the head (not including the tentacles), the anterior margin of the shell aperture and the most posterior part of the foot. These points were digitised every 5 s during the trial. For the angle between the tentacles, three points were digitised: the distal tip of each optic tentacle and the point where the mid-lines of the tentacles would intersect (tentacles were straight). Trials were analysed for: time in each quadrant, path of snail at 5-s intervals and tentacle positions every 60 s during the trial. The angle between the tentacles was averaged for each snail and across all snails. Also, the time of trial and final location of the snail were recorded. Average velocity of each snail was calculated at 20-s intervals.

Results and discussion

All snails moved for the duration of their trial and went directly to the odour source. Two of the trials in which the snails went directly to the odour source were conducted in the dark and at night (Trials 2 and 3), while the other trial (Trial 1) was conducted in light and before sundown. All snails spent the majority, if not all, of their time in the quadrant with the odour source and their paths were analysed for direction and to observe head movements (Fig. 2). The overall average angle between tentacles was 102° with a standard deviation of 22° (n = 37, range 63°–165°, where n is the number of measurements used to calculate the mean). The three snails differed in tentacle angle with mean ± s.d. of 89° ± 8° (n = 5), 101° ± 15° (n = 15) and 107° ± 28° (n = 17). The average velocity of the snails was plotted against distance to the odour source (Fig. 3).

All snails used in this experiment moved directly to the odour source. This shows strong preliminary evidence that *M. gulosum* is able to track food odours accurately in air and

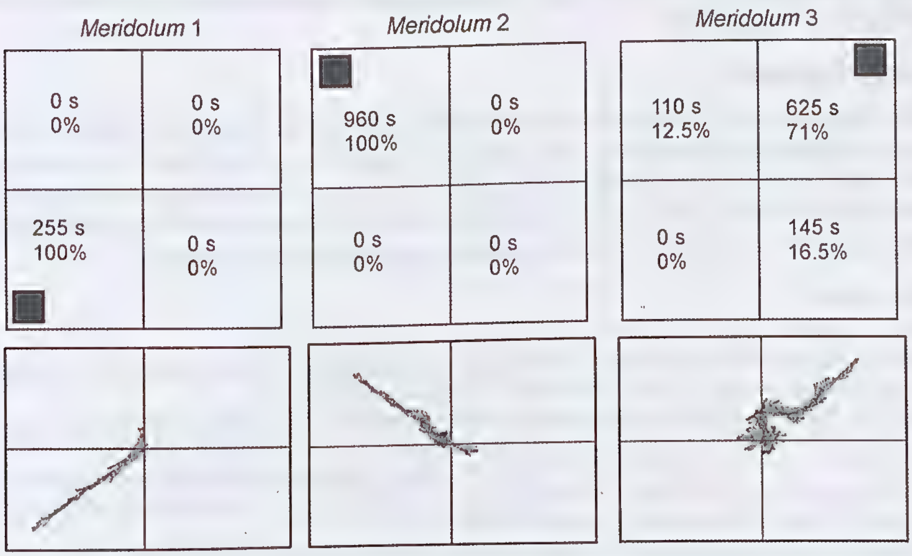

Fig. 2. Results of time in quadrant test (top arenas) and path analysis (bottom arenas) for *Meridolum gulosum*. The solid black box indicates location of the odour source. Snails were started at the centre of the arena. Paths (below) show snail positions every 5 s of head, middle and foot (black dots) connected by a line.

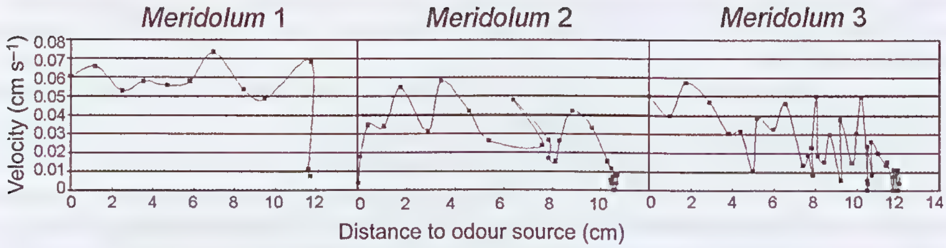

Fig. 3. Average velocity at 20-s intervals against distance to odour source.

probably uses chemoreception to find food sources. In each trial, the snail started moving slowly but showed an increase in velocity when within 10 cm of the odour source. This implies that *M. gulosum* can detect odours from at least 10 cm away (Fig. 3).

It has been shown by Chase and Croll (1981) that the optic tentacles of stylommatophoran pulmonates are capable of detecting airborne odours. The optic tentacles of *M. gulosum* were held at a characteristic angle, which may be helpful in comparing a gradient of odour between the right and left optic tentacles. The oral tentacles of *M. gulosum* were tapped alternately whenever the snail was crawling, although they were not visible on the video and could not be analysed. Further studies of the movements of the tentacles while odour tracking would increase our understanding of how gastropods track chemical plumes in air.

The odour tracking abilities of gastropods also enable them to be agricultural pests; snails like the European garden snail *Cantareus aspersus* can find plant food through chemoreception (Farkas and Shorey 1976). The movements of the tentacles while tracking plant odours were characterised in *Cantareus aspersus*, showing the average angle between the tentacles was 115° (n = 5) (calculated from Lemaire and Chase 1998). A better understanding of the mechanisms used in long-distance chemoreception could assist in the control of such gastropods.

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New Taxon

Microeledone mangoldi n. gen. and n. sp., a deep-water pygmy octopus from the Norfolk Ridge, New Caledonia (Cephalopoda: Octopodidae)

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Abstract

Microeledone mangoldi n. gen. and n. sp. is described from a male specimen collected from approximately one kilometre deep on the Norfolk Ridge south of New Caledonia in the south-west Pacific Ocean. This tiny octopus is characterised by a single row of suckers that are functional to the tips of the arms, the absence of an ink sac, the presence of a pair of chitinous stylets, a UU-shaped funnel organ, a copulatory organ with distinct ligula and calamus, and a distinctive radula. The radula has seven teeth per row. The unique central (rachidian) tooth has a long, sharp mesocone with a curved and grooved tip. The remaining rows of teeth are also unique, being flattened and plate-like. Marginal plates are absent. The body is smooth, without papillae, cartilaginous tubercles, or a lateral ridge. Functional chromatophores are absent. This octopus appears related to several other genera of deep-sea octopods with a single row of suckers, namely *Thaumeledone* Robson, 1930, *Bentheledone* Robson, 1932 and *Graneledone* Joubin, 1918, to which the new genus is compared. Definitions of the genus *Thaumeledone* are reviewed.

Additional keywords: deep-sea, Indo-Pacific, taxonomy.

Introduction

A distinctive new genus and species of octopus, *Microeledone mangoldi*, is reported from deep-water in the south-west Pacific Ocean. This new taxon is represented by a single submature male captured at a depth of ~1000 m in the Coral Sea, south of New Caledonia on the northern end of the Norfolk Ridge. This region of the Pacific Ocean is largely a bathyal plain dotted with submarine mountain ranges and isolated seamounts. Recent research into the deep-sea faunas of these poorly known habitats has uncovered highly diverse and largely unknown assemblages of organisms, many of which are endemic (Bouchet and Metivier 1982; Richer de Forges 1990; Richer de Forges *et al.* 2000; Valdéz 2001*a*, 2001*b*; Valdéz and Gosliner 2001).

The new taxon is described herein and compared with other octopods sharing similar morphological features. Geographic and phylogenetic aspects are discussed, particularly in relation to the Australian, New Zealand, and Antarctic deep-sea octopod fauna.

Material and methods

The single specimen described in this paper was collected in 1993 during a joint French cruise of ORSTOM and the Muséum National d'Histoire Naturelle (Paris) to New Caledonia and surrounding areas of the Coral Sea. It was captured with a beam trawl on the Bathus 3 Expedition at 980–1000 m depth on the northern end of the Norfolk Ridge. The preserved specimen is housed in the collections of the museum in Paris (MNHN). Additional species were examined from the collections of Museum Victoria, Melbourne, Australia (MV), The Natural History Museum, London, UK (BMNH), National Museum of Natural

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History, Washington, DC, USA (USNM), Royal Museum of Natural History, Brussels, Belgium (MRHNB) and South African Museum, Cape Town, South Africa (SAM).

The taxonomic methodology and diagnostic characters used in the description below follow Norman and Sweeney (1997) and Norman *et al.* (1997).

Systematic descriptions

Family **OCTOPODIDAE** d'Orbigny, 1840

Microeledone n. gen.

Type species: *Microeledone mangoldi*, by monotypy.

Diagnosis

Small robust octopus; mantle muscular, roughly spherical; mantle aperture moderate (~40% of neck circumference); funnel organ large, UU-shaped, limbs of equal length with sharp tips; interbrachial aquiferous (water) pore system absent; stylets long, chitinous; eyes large; gills with 4–5 (typically five) lamellae per demibranch plus terminal lamella; arms robust, short, equal in length; arm autotomy absent; suckers uniserial, closely set; suckers normal, functional to tips of all arms, without modification except for hectocotylized arm of males; enlarged suckers absent; right arm III hectocotylized, shorter than opposite arm; copulatory organ with distinct ligula and large calamus; crop with distinct swelling but without anterior directed diverticulum; posterior salivary glands large, length similar to buccal mass; ink sac absent; intestine short, tapered, with single bend. Radula with serial rows of seven teeth; marginal plates absent. Rachidian teeth broad-based with elongate sickle-shaped mesocone with grooved anterior face. Other teeth flattened and blade-like, without obvious sharp cusps. Terminal organ (penis) short and straight with simple diverticulum. Skin smooth; papillae and lateral ridge absent; functional chromatophores absent, uniformly pink-grey in colour.

Remarks

Spermatophores of the species are unknown. Females unknown.

Erection of this new genus is based on the following unique suite of diagnostic characters: (*1*) small size at maturity; (*2*) suckers uniserial; (*3*) suckers at tips of arms in male are not modified; (*4*) radula with seven teeth per row, rachidian teeth with sickle-like elongate and grooved mesocone, other teeth flattened and blade-like, marginal plates absent; (*5*) copulatory organ with distinct ligula and calamus; (*6*) funnel organ large and UU-shaped; (*7*) webs are deep between all arms; (*8*) posterior salivary glands are very large; (*9*) crop swollen but without anterior diverticulum; (*10*) ink sac and anal flaps are absent; (*11*) skin smooth without texture or lateral ridge; and (*12*) functional chromatophores are absent and body appears relatively unpigmented.

Etymology

From the Greek *micros*, meaning 'small' in reference to the size of the animal.

Microeledone mangoldi n. sp.

(Figs 1–4; Table 1)

Material examined

Holotype. 18 mm ML male; south-west Pacific Ocean, Coral Sea, south of New Caledonia, northern end of Norfolk Ridge, 23°23′S, 167°52′E, 980–1000 m, 29 Nov. 1993, coll. P. Bouchet, B. Richer de Forges

and A. Warén, N/O *Alis*, cruise Bathus 3, station C-P823, beam trawl (MNHN 2105). Additional material examined are listed in Appendix 1.

Diagnosis (with characters of genus except as noted below)

Octopus small (mantle length 18 mm); arms short (1.3× mantle length). Webs deep and fleshy, extend almost half of arm length (deepest 45.8% of longest arm); dorsal and lateral webs equal in depth, ventral web shallowest. Sucker counts on normal arms 31–32; 22 suckers on hectocotylized arm of male. Male hectocotylized arm short (71% length of opposite arm); ligula small (*c.* 8% of hectocotylized arm length in submature male), copulatory groove wide and open; calamus large, wide (46% of ligula length); terminal organ short and straight with simple diverticulum. Skin colour uniform pink-grey with dark maroon pigment in oral webs for proximal third of arms.

Description

The following description is based on the only known specimen, a submature male in good condition, fixed in formalin and preserved in 70% ethanol. Counts and measurements for this specimen are presented in Table 1. Relative indices are presented in the text.

Animal small, fleshy and robust (mantle length, 18 mm; total length, 46 mm; total body wet weight, 3.2 g). Mantle round (Fig. 1*a*); body wall relatively thick, muscular; skin thick, soft and semi-gelatinous. Mantle width almost equal to mantle length (index 92.8%). Head wide, slightly narrower than mantle width (index 82.9%). Eyes large. Stylets present (Fig. 1*b*), large (33.7% of mantle length), chitinous. Pallial aperture less than half mantle circumference (index *c.* 40%). Funnel short (35.4% of mantle length), wide; elongate lateral pouches present; free about one-third length of funnel (index 34.4%). Funnel organ (Fig. 1*c*) UU-shaped, located towards anterior end of dorsal funnel; anterior tips sharply pointed; organ large, occupies over half length of funnel (index 57.8%); lateral and medial limbs equal in length (index 97.3%).

Webs fleshy, deep (45.8% of longest arm); equal in depth except for ventral sector (formula A = B = C = D > E); web margins absent.

Arms short (longest 1.3× mantle length); robust (arm at widest point 16.0% of mantle length); roughly triangular in cross-section (with single sucker row as apex), taper evenly in width from arm base to distal tip. Arms equal in length. Arm autotomy absent. Suckers small (diameter of largest 5.0% of mantle length); tightly packed in single row (slightly bunched into zig-zag arrangement towards distal end of some arms); suckers slightly elevated, rim thickened, infundibulum narrow, acetabulum small. Suckers functional (but very small) to distal tips of normal arms. Enlarged suckers absent in single submature male specimen. Sucker counts on all normal arms 31–32; hectocotylized arm with 22 suckers.

Right arm III hectocotylized in males (70.8% of opposite arm length; 93.9% of mantle length). Copulatory organ (Fig. 1*d*) of moderate size relative to arm length (7.6% of hectocotylized arm length). Ligula wide with wide copulatory groove; calamus large, open (46% of ligula length). Spermatophore groove shallow, fleshy.

Gills with 4–5 lamellae per outer and inner demibranch; lamellae of inner demibranchs reduced in length, distinctly shorter than outer lamellae (index ~60%).

Digestive tract (Fig. 2*a*). Buccal mass large, about one-third length of mantle (index 33.7%); almost as large as digestive gland (index 80.3%). Anterior salivary glands relatively small, approximately one-quarter length of buccal mass (index 26.2%); posterior salivary glands very large, almost as long as buccal mass (index 88.5%) and three-quarters length of digestive gland (index 71.1%). Oesophagus short; crop distinctly swollen but

Table 1. *Microeledone mangoldi* n. gen. & n. sp., counts and measurements (mm) of the holotype

A–E, designation of web sectors from dorsal to ventral; 1–4 arm pairs numbered from dorsal to ventral

Sex	Male
Maturity	Submature
Total length	46
Total wet weight (g)	3.2
Dorsal mantle length	18
Ventral mantle length	16
Mantle width	17
Head width	15
Funnel length	6.4
Free funnel length	2.2
Funnel organ length	
Lateral limb	3.6
Medial limb	3.7
Web depth	11
A	11
B	Left = 11, right = 11
C	Left = 11, right = 10
D	Left = 11, right = 7[A]
E	7
Web depth formula	A = B = C = D > E
Arm lengths	
1	Left = 23, right = 23
2	Left = 24, right = 23
3/Hc	Left = 24, right = 17
4	Left = 22, right = 22
Arm length formula	Equal
Arm width	2.9
Sucker diameter	0.9
Sucker counts	
1	Left = 31, right = 31
2	Left = 31, right = 32
3/Hc	Left = 31, right = 22
4	Left = 31, right = 32
Gill count (outer/inner demibranch)	Left 5/5, 4/5
Stylet length	Left 6, right –
Ligula length	1.3
Calamus length	0.6
Terminal organ length	2.4
Diverticulum length	0.7

[A]Includes spermatophore guide.
Hc, hectocotylized right arm of male.

without diverticulum. Stomach bipartite; caecum with less than one whorl, ducts to digestive gland (pancreas) short and wide. Intestine short, broad, very wide at point of attachment to caecum, tapers to narrow, thin-walled rectum. Digestive gland ovoid with slightly elongate posterior lobes; pancreas present as small patch of light-coloured tissue at point of entry of ducts into digestive gland. Ink sac absent. Anal flaps absent.

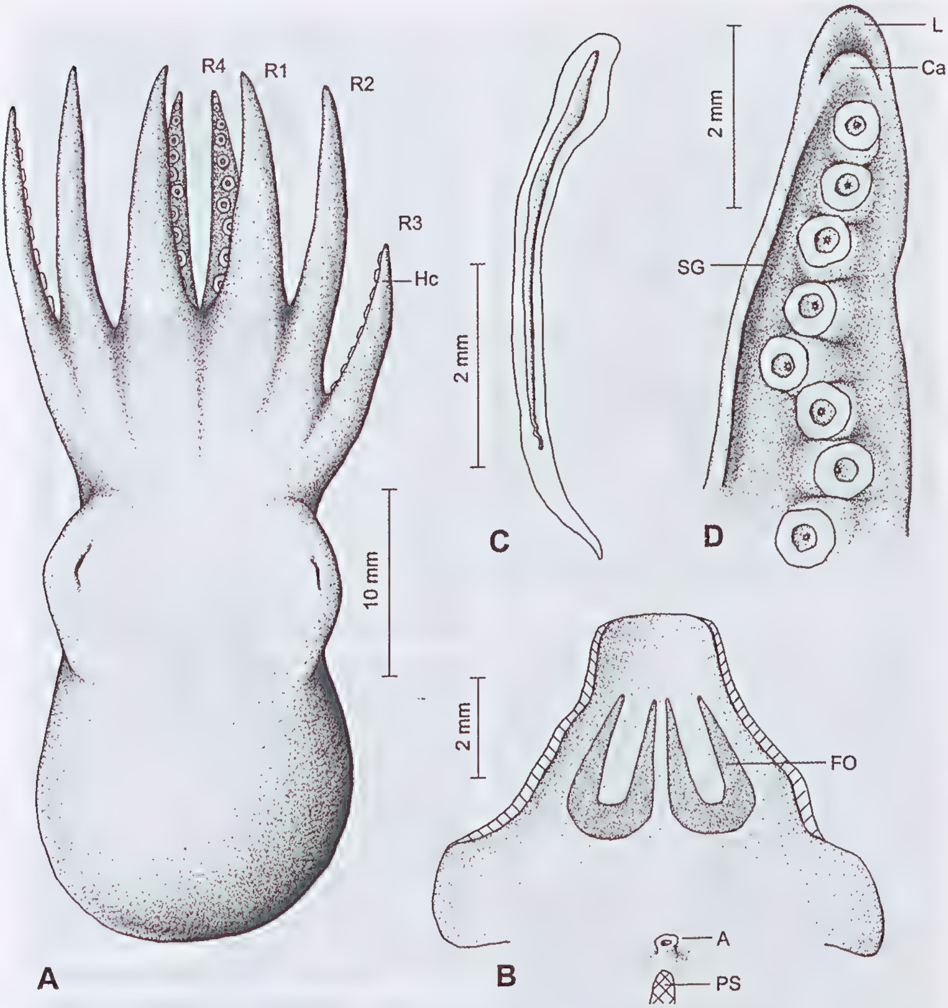

Fig. 1. *Microeledone mangoldi* n. gen. and n. sp. *a–d*, male holotype (18 mm ML, MNHN 2105). *a*, dorsal view of whole animal; *b*, stylet (right side) within shell sac; *c*, funnel cut open to display funnel organ *in situ*; *d*, distal end of male hectocotylized arm with copulatory organ, oral view. A, anus; Ca, calamus; FO, funnel organ; Hc, hectocotylized arm; L, ligula; PS, pallial septum (cut); R1–4, right arms 1 to 4; SG, spermatophore groove. Scale bars: *a*, 10 mm; *b–d*, 2 mm.

Upper beak (Fig. 2*b*) hood of moderate size, almost half of beak length (index 46.0%); rostrum bluntly hooked, cutting edge rounded; crest slightly rounded. Lower beak (Fig. 2*c*, *d*), hood and crest slightly rounded; rostrum pointed, cutting edge sharp; lateral walls parallel with slightly concave posterior margin. Radula (Fig. 3) with seven teeth per transverse row; marginal plates absent. Rachidian tooth acuspid, with broad base; mesocone sickle-shaped and blade-like (elongate, curved and flattened), oriented perpendicular to main axis of radular ribbon. Other teeth flattened, plate-like (Fig. 3*e*). First lateral teeth small, elongate, rectangular to square in shape; acuspid. Second lateral teeth triangular, rounded, swollen at medial end; acuspid. First marginal teeth slightly curved to triangular with blunt medial tip; acuspid.

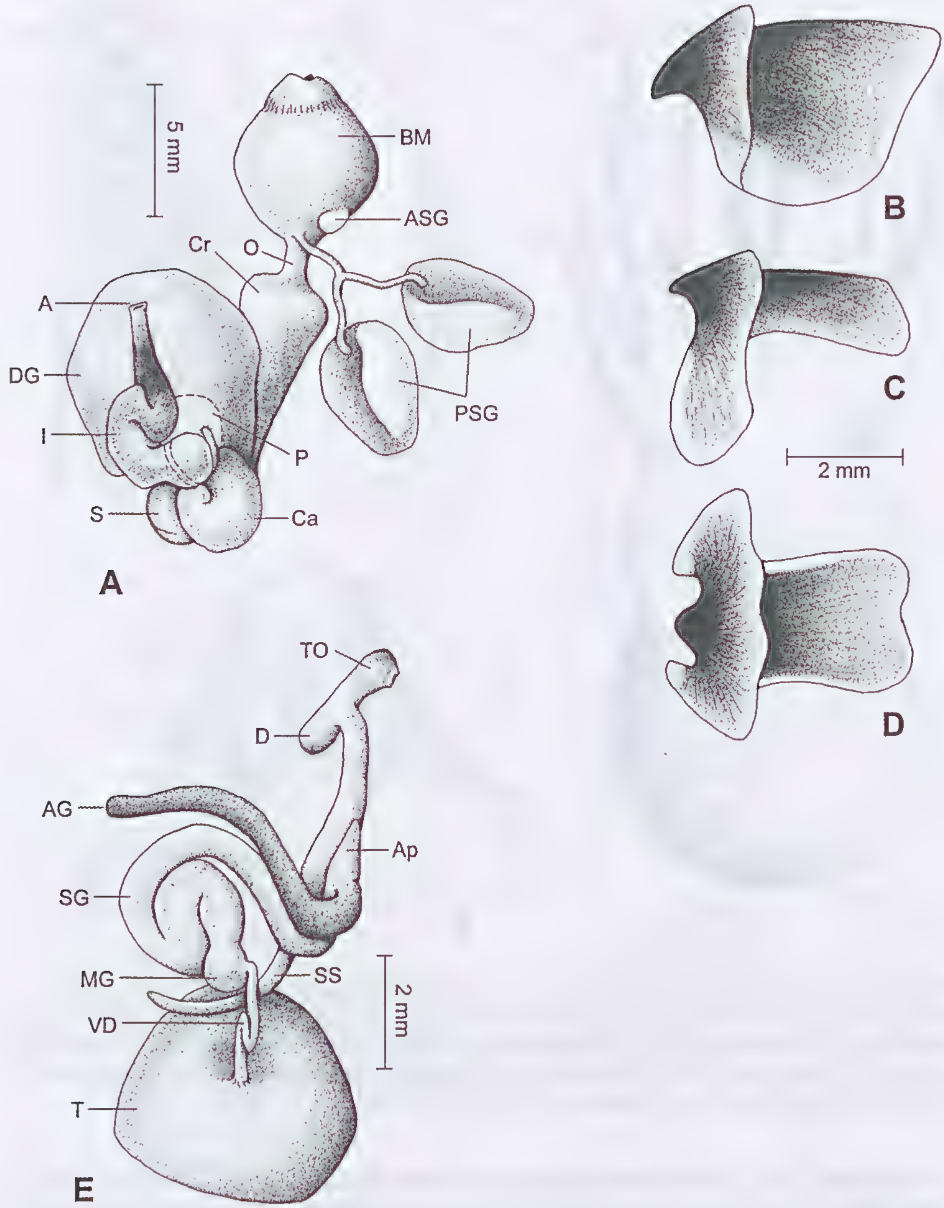

Fig. 2. *Microeledone mangoldi* n. gen. and n. sp. *a–e*, digestive and reproductive systems (male holotype, 18 mm ML, MNHN 2105). *a*, digestive tract; *b*, upper beak, lateral view; *c*, lower beak, lateral view; *d*, lower beak, ventral view; *e*, reproductive tract, ventral view. A, anus; Ap, appendix; AG, accessory gland; ASG, anterior salivary gland; BM, buccal mass; Ca, caecum; Cr, crop; D, diverticulum; DG, digestive gland; I, intestine; MG, mucilaginous gland; O, oesophagus; P, pancreas; PSG, posterior salivary gland; S, stomach; SG, spermatophoric gland; SS, spermatophore storage sac; T, testis; TO, terminal organ; VD, vas deferens. Scale bars: *a*, 5 mm; *b–e*, 2 mm.

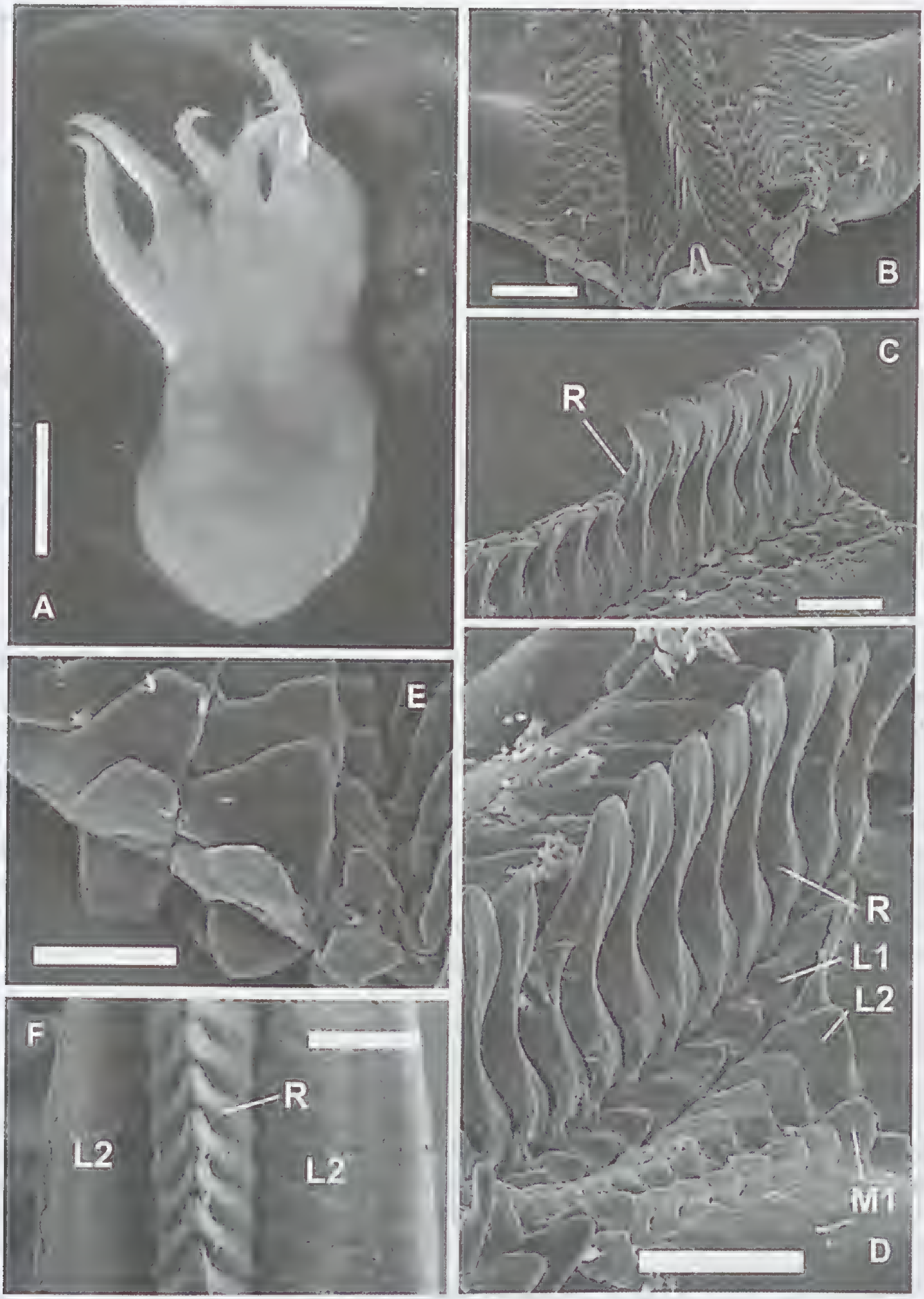

Fig. 3. *Microeledone mangoldi* n. gen. and n. sp. *a–f*, photographs of holotype and radula (18 mm ML male, MNHN 2105). *a*, dorsal view of whole animal; *b–e*, scanning electron micrographs of radula; *b*, anterior view of radula; *c*, anterior lateral view of broken and intact rachidian tooth row showing curved and grooved tips; *d*, anterior lateral view of radula showing tooth nomenclature; *e*, close up of first marginal tooth (left), second lateral tooth (centre) and first lateral tooth (right); *f*, radula of *Thaumeledone gunteri* (MV F65706). L1, first lateral tooth; L2, second lateral tooth; M1, first marginal tooth; R, rachidian tooth. Scale bars: *a*, 10 mm; *b–d*, 0.1 mm; *e* = 50 μm; *f* = 0.2 mm.

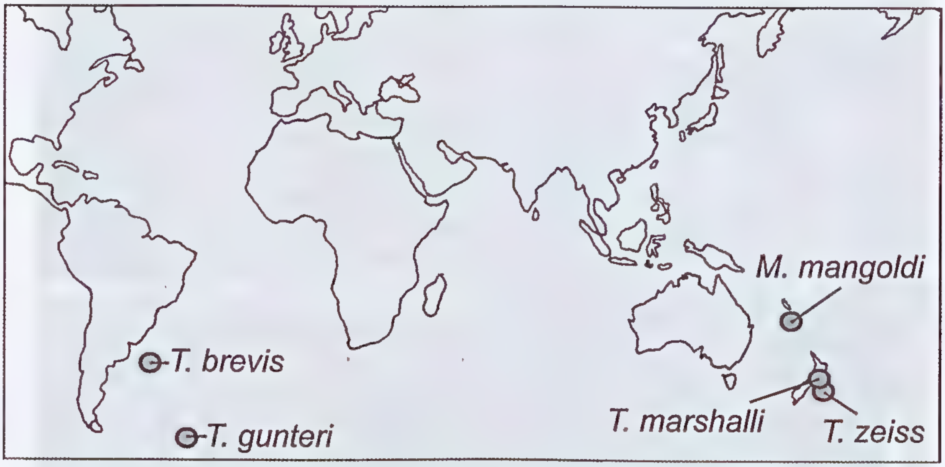

Fig. 4. *Microeledone mangoldi* n. gen. and n. sp. Collection locality of only known specimen, and type localities of other species assigned to the genus *Thaumeledone*.

Reproductive tract of submature male (Fig. 2*g*). Terminal organ linear, short (13.2% of mantle length); diverticulum small (29.2% of organ length); genital aperture subterminal. Appendix present at junction of accessory gland, spermatophoric duct and spermatophore storage sac. Spermatophores unknown.

Females unknown.

Colour of live animal unknown. Preserved specimen uniform light pink-grey in colour on both dorsal and ventral surfaces. Oral web dark maroon in colour for proximal third of arms. Functional chromatophores not evident. Crop, posterior salivary glands, stomach, and distal two-thirds of intestine enclosed within darkly-pigmented (maroon) membrane. Skin smooth without apparent tuberculate, granular, or papillate texture; patch and groove system absent.

Distribution

Known only from the type locality (Fig. 4).

Life history

Nothing is known about the life history or behaviour of this rare species. Numerous prey remains were found in the stomach. Contents included setae and at least seven jaw fragments from polychaetes, and the radula of an unidentified gastropod mollusc. Foraminiferans (whole and broken) and sand grains were present, most likely ingested incidentally along with other prey.

Externally, the proximal oral surfaces of the webs between the arms are darkly pigmented. In addition, sheaths of dark maroon pigmented tissue envelop the salivary glands, crop, stomach, and part of the intestine. This suggests the animal's ability to mask out light produced during the capture and ingestion of luminescent prey. Other deep sea octopods are similarly pigmented both externally and internally (e.g. *Benthoctopus karubar*, see Norman *et al.* 1997).

Oocysts of the apicomplexan parasite *Aggregata* were present in large numbers throughout the digestive tract, especially caecum and proximal intestine. This indicates that

the animal had presumably fed extensively on crustaceans, known to be the intermediate hosts for this protozoan parasite (see Hochberg 1990).

Etymology

Named in honour of our late colleague and friend the eminent cephalopod researcher Dr Katharina M. Mangold (1922–2003). For many years she was Directeur de Recherche at the Laboratoire Arago, Banyuls-sur-Mer, France.

Common name

Sickletooth pygmy eledone.

Discussion

Taxonomy

Four morphological features characterise this interesting octopus and distinguish it from other known octopuses of both shallow and deep waters: (*1*) a single row of suckers; (*2*) loss of ink sac; (*3*) distinctive and unique radula; and (*4*) small size.

Sucker rows

The majority of benthic octopus species (>90% of nominal species) possess two rows of suckers. The following genera possess a single row of suckers: *Adelieledone* Allcock *et al.*, (2003); *Bentheledone* Robson, 1932; *Eledone* Leach, 1817; *Graneledone* Joubin, 1918; *Megaleledone* Taki, 1961; *Pareledone* Robson, 1932; *Tetracheledone* Voss, 1955; *Thaumeledone* Robson, 1930; *Velodona* Chun, 1915 and *Vosseledone* Palacio, 1978.

Loss of ink sac

Many deep-sea octopuses lack a functional ink sac, ink having less value in lightless depths (Voss 1988*a*). Of the taxa that possess a single row of suckers, only three genera lack an ink sac: namely *Graneledone*, *Bentheledone* and *Thaumeledone*.

Radula

The most distinctive feature of the new octopus described herein is the radula. It consists of seven teeth per row but lacks marginal plates. The mesocone of the rachidian tooth is modified into a vertically-oriented sickle-shaped structure with a grooved anterior surface (Fig. 3*c*). All other teeth are flattened and blade-like. The only other octopus with a radula that contains blade-like structures is *Vosseledone charrua* Palacio, 1978. In *Vosseledone* the rachidian tooth is modified into a trident of wide transverse blades, more suited to scraping.

Size

Microeledone mangoldi is the smallest octopus species described to date with a uniserial arrangement of suckers. The male specimen is close to mature at a mantle length of 18 mm and total body wet weight of 3.2 g. Although the testes were well developed, spermatophores were not present. The modified tip of the third right arm of this animal is well developed with a distinct ligula and calamus.

Primary differences between *Microeledone* and other octopodids with a single row of suckers are summarised in Table 2. The genera that appear to be most closely related in form to *Microeledone* are *Graneledone, Bentheledone* and *Thaumeledone*. All are easily distinguished from the new genus.

Table 2. ***Microeledone mangoldi*** **n. gen. & n. sp., comparison with other octopus genera that possess a single row of suckers on the arms**
Terminology for vertical distribution and associated depth ranges: abysso, abyssobenthic (> 2500 m); bathy, bathybenthic (1000–2500 m); epi, epibenthic (0–200 m); meso, mesobenthic (200–1000 m)

Character	*Microeledone*	*Thaumeledone*[A]	*Bentheledone*	*Graneledone*	*Megaleledone*	*Pareledone*	*Adelieledone*	*Tetracheledone*	*Velodona*	*Vosseledone*	*Eledone*	*'Eledone'*
Source material	See 'Material examined'	See 'Material examined'	See 'Material examined'	Joubin 1918; Robson 1932; Voss and Pearcey 1990	Taki 1961; Lu and Stranks 1994	Lu and Stranks 1994; Allcock *et al.* 2003	Allcock *et al.* 2003	See 'Material examined'	See 'Material examined'	Palacio 1978	See 'Material examined'	Norman *et al.* 1997
No. species	1	2+	2+	8+	1	7+	3	1	1	1	4	1
Genotype	*M. mangoldi*	*T. brevis*	*B. rotunda*	*G. verrucosa*	*M. setebos*	*P. charcoti*	*A. adelieana*	*T. spinicirrus*	*V. tongata*	*V. charrua*	*E. cirrhosa*	*E. palari*
Depth range	Meso	Meso-abysso	Abysso	Meso-abysso	Epi-meso	Epi-meso	Epi	Meso	Meso	Epi	Epi-meso	Epi-meso
Ink sac	Absent	Absent	Absent	Absent	Reduced	Present	Present	Present	Present	Present	Present	Present
Gill count	4–5	4–5	4–5	6–9	10–11	6–11	7–8	6–9	8	6–7	8–13	5
Arm length	1.3	1.3–1.5	2–3	2.1–4.2	2.0–2.6	1.5–3.6	1.5–2.7	1.5–2.4	3–4.5	1.9–2.5	1.8–4.5	1.5–2
Web	46	41–50	29–43	17–37	40–45	20–50	25–37	43–45	18–26	34	20–37	38–67
Stylets	Present	Present	NI	Absent	Absent	Present	Absent	Present	Present	Unknown	Present	Present
Radula teeth per row	7	3–5	7	7	7	7	7	7	7	3	7	7
Rachidian modifications	Elongate homodont, concave tip	Homodont	Homodont	Homodont	Homodont	Normal	Normal	Normal	Normal	Trident blades	Normal	Normal
Crop diverticulum	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Present	Present	Present
Posterior salivary glands	Large	Moderate	NI	Small to tiny	Moderate	Moderate	Very large	Moderate	Moderate	Moderate	Large	Large
Funnel organ	UU	VV, IIII	Wide V in *B. albida*	VV	UU	UU	W	IIII	VV	VV	UU/W	UU
Ligula	Normal with calamus	Normal with calamus	Normal with calamus	Normal with calamus	Normal with calamus	Normal with calamus	Normal with calamus	Normal with calamus	Normal with calamus	Normal with calamus	Spongy or no calamus	Normal with calamus
Male arm tip modifications	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Ridges or fingers	Spongy tissue
Lateral ridges on mantle	Absent	Absent	Absent	Absent	Present	Present or absent	Absent	Present	Absent	Absent	Present or absent	Present
Skin texture	Smooth	Low papillae	Smooth	Cartilaginous warts	Low papillae	Papillae	Scattered papillae	Spiked papillae	Regular papillae	Low papillae	Patch and groove	Low papillae

[A]Excludes O'Shea 1999 species: *T. marshalli* and *T. zeiss* (see 'Discussion' and Table 3).
NI, not indicated.

Table 3. ***Microeledone mangoldi*** **n. gen. & n. sp, comparison with three other species currently referred to the genus** ***Thaumeledone***

Characters	*M. mangoldi*	*T. brevis*	*T. gunteri*	*'T'. zeiss*	*'T'. marshalli*
Ink sac	Absent	Absent	Absent	Absent	Absent
Crop: anterior diverticulum	Absent	Absent	Absent	Absent	Absent
Radula					
Teeth per transverse row	7	3	5	7	5
Marginal plate	Absent	Absent	Absent	Present	Absent
Rachidian mesocone	Blade-like	Absent	Triangular	Triangular	Triangular
Gill lamellae counts	4–5	4–5	4–5	4–5	5
Eye size	Large	Large	Large	Large	Large
Stylets	Present	NI	Present	NI	NI
Funnel organ shape	UU	IIII	VV	VV	VV
Posterior salivary glands (% buccal mass)	Very large (89)	Large	Large	Large (72)	Large (72)
Arm lengths (x ML)	1.3	~1.7	1.4–1.5	1.0–1.4	1.2–1.3
Web depths (% longest arm)	46	68	41–51	38–53	50–65
Web margins	Absent	NI	3/4 length	Absent	Absent
Sucker diameter (% ML)	5	5	7–8	4–5	4–7
Enlarged suckers: males	Absent	NA (female only)	Absent	Absent	Absent
Sucker counts					
Normal arms	31–32	25–29	35–36	29–33	28–31
Hectocotylized	22	NA (female only)	22	19	17–20
Modified arm tips: males	Absent	NA (female only)	Absent	Absent	Absent
Ligula: shape	Normal ligula and calamus	Female only	Normal	Normal	Normal
Skin sculpture	Smooth	Papillose	Papillose	Papillose	Smooth/faint
Lateral ridge	Absent	Absent	Absent	Absent	Absent
Papillae: supra-ocular	Absent	Present	Absent	Present (2)	Absent
Reverse counter-shading	Absent	NI	Present	Present	Present
Dark oral web	Proximal 1/3	Present	All	All	All
Type locality	Norfolk Ridge, New Caledonia	S. Atlantic, SE of Uruguay	Antarctica, S. Georgia I.	Chatham Rise, New Zealand	Chatham Rise, New Zealand
Latitude	23°S	37°S	53°S	44–45°S	37–42°S
Longitude	168°E	~54°W	35°W	173–178°E	176–177°E
Depth (m)	980–1000	1096	400	1050–1400	2000–2500

NA, not applicable; NI, not indicated

Microeledone resembles *Graneledone* in that they both lack an ink sac and an anterior directed crop diverticulum. *Graneledone* is clearly distinguished by the presence of numerous raised cartilaginous tubercles on the body and arms, and longer arms (2–5× the mantle length *v.* 1.3).

Microeledone is similar to *Bentheledone* in the absences of body texture, ink sac and anterior-directed crop diverticulum. *Bentheledone*, however, differs in having a single broad V-shaped funnel organ (*v.* UU), small eyes (*v.* large), very small posterior salivary glands (*v.* large), and longer arms (2–3× the mantle length *v.* 1.3). The genus *Bentheledone* is in critical need of detailed study.

The taxa most similar to *Microeledone mangoldi* have been placed in the genus *Thaumeledone* (Table 3). This genus was originally erected by Robson (1930) on the basis of a degenerate radula with only a single tooth per transverse row, gill counts of 5–6 lamellae, and short subequal arms with very deep webs. Robson included two species in this genus, *T. brevis* (Hoyle, 1885) and *T. gunteri* Robson, 1930. Both species had characters that challenged Robson's own generic diagnosis, i.e. *T. brevis* had 4–5 gill lamellae and *T. gunteri* had a radula with 'faint traces of admedians and of an oblong second lateral with a low cusp' (Robson 1932: 317). Voss (1988*a*) amended Robson's generic diagnosis reporting the presence of marginal plates on the radula and adding three new characters: a tall and narrow VV funnel organ (despite IIII reported for *T. brevis*), vestigial posterior salivary glands, and a papillose dorsum.

The typical radula for most members of the family Octopodidae consists of seven teeth per transverse row plus adjoining marginal plates. Terminology for these teeth are as follows: *rachidian* (R): this single central tooth typically has a tall medial mesocone that may lack cusps ('acuspid'), bear a single cusp ('unicuspid') or multiple cusps ('multicuspid'); *first laterals* (L1): typically a small low tooth with a single cusp; *second laterals* (L2): typically a larger curved tooth with a single cusp towards the medial end of the tooth; *first marginals* (M1): an elongate and curved tooth; and *marginal plates* (MP): square to oblong plates lacking cusps and anchored within the radula tissue.

In *Thaumeledone brevis* and *T. gunteri* the radula is considered degenerate: only 3–5 teeth are present in a transverse row. Figure 3*f* shows the radula of *Thaumeledone gunteri* with three visible teeth per row: the central unicuspidate rachidian row, and two rows of large and flattened lateral teeth. Robson (1932: 317) reported that *T. gunteri* showed 'faint traces of *admedians* (= first lateral teeth) and of an oblong second lateral with a low cusp'. We concur with Robson in considering the large flattened tooth to be a highly modified second lateral tooth. There has been some confusion in the literature in the interpretation of this flattened wide tooth. We believe Voss (1988*a*) incorrectly defined this tooth as a marginal plate, hence adding this character to the generic diagnosis.

In order to incorporate two new taxa from New Zealand waters (*T. marshalli* and *T. zeiss*) O'Shea (1999: 246) further amended the diagnosis for *Thaumeledone* as reproduced here:

> 'Small-bodied muscular benthic octopodids characterised by papillose dorsal and ventral surfaces of mantle, head, arms and web; arms short; non-hectocotylised (*sic*) arm sucker counts very low (less than 20); non-hectocotylised arm sucker counts very low, less than 40 at maturity; penis diverticulum hammer-shaped, with or without pronounced spiral; distal oviducts expanded, length less than or equal to that of proximal oviducts. Posterior salivary glands large to small; radula dentition simple, rachidian without lateral cusps, marginal plates present; lateral teeth vestigial to absent; funnel organ VV; outer gill lamellae few, 4 or 5, inner demibranch little reduced (amended from Voss, 1988)'.

Many of the characters within O'Shea's (1999) generic diagnosis for *Thaumeledone* are problematic. Several character states contradict descriptions and illustrations that O'Shea provides, both for existing members of this genus and his new included species, for example: (*1*) '*papillose dorsal and ventral surfaces of mantle, head, arms and web*' (yet *T. marshalli* is reported as 'entire animal smooth or with extremely faint traces of papillation' (p. 252)); (*2*) '*distal oviducts .... length less than or equal to that of proximal oviducts*' (yet distal oviducts are longer than the proximal oviducts in O'Shea's fig. 153*E* of

the holotype of *T. gunteri*); (*3*) *'marginal plates present'* (O'Shea's illustration of the radula of *T. marshalli* appears analogous to that of *T. gunteri* with reduced first lateral tooth and a broad and flattened second lateral tooth. As such we would interpret this radula as lacking marginal plates. In describing the lateral teeth of *T. marshalli*, O'Shea does not distinguish between the marginal plate or first marginal tooth, simply referring to it as: 'single block-like marginal.'); (*4*) *'lateral teeth vestigial to absent'* (*T. zeiss* possesses the full compliment of seven teeth per row, none of which appear reduced in size. The second lateral teeth in *T. marshalli* appear very well developed, as stated above).

Certain characters within O'Shea's diagnosis offer little diagnostic value, namely: (*1*) penis diverticulum hammer-shaped, with or without pronounced spiral; and (*2*) posterior salivary glands large to small.

As illustrated by O'Shea (1999: 261), the character of vestigial posterior salivary glands does not hold true for either the syntype of *T. brevis* or the holotype of *T. gunteri*. The glands of both are smaller than that of *Microeledone* but hardly constitute vestigial organs (such organs being reported for other, non-type material attributed by Voss to *Thaumeledone*, see O'Shea). As a consequence it is appropriate that this character should be removed from the diagnosis.

It appears that O'Shea found it difficult to place his two new taxa in existing genera. As a consequence he emended and broadened the diagnosis of *Thaumeledone* to include these New Zealand species. His concluding remarks make this apparent: 'As *T. zeiss* and *T. marshalli* are not particularly alike, and because equally dissimilar species are found in southern oceans, it is possible that two genera exist amongst this complex of small-bodied, short-armed species (with low total arm-sucker counts)…' (1999: 255).

We do not agree that the definition of *Thaumeledone* should be modified to accommodate O'Shea's new taxa. If O'Shea's diagnosis truly encompassed his two species as well as *T. brevis* and *T. gunteri*, the diagnosis would be left with no diagnostic characters other than short arms, low sucker counts and a VV funnel organ (that does not encompass the IIII funnel organ reported for *T. brevis*). Similarities suggest that there may be phylogenetic affinities amongst the suite of small southern hemisphere species that possess a single row of suckers (including our new taxon); however, excessive modifications to the diagnosis of *Thaumeledone* have resulted in one that lacks any real distinguishing diagnostic characters.

In light of these partial (and questionable) revisions to the genus, it is clear that there are few remaining characters that diagnose *Thaumeledone*. As a consequence we choose to restrict the diagnosis of *Thaumeledone* to include both taxa originally placed within this genus (*T. brevis* and *T. gunteri*) based on the following core characters: (*A*) degenerate radula, reduced number of teeth (3–5) per transverse row; (*B*) papillose skin; (*C*) tall and narrow VV funnel organ or four separate linear components (IIII): (*D*) low gill counts (4–6 per demibranch); (*E*) short arms (1–1.7× ML); and (*F*) deep webs (~30–60% longest arm).

If we restrict our consideration to these characters, *Microeledone* is similar to *Thaumeledone* in having short subequal arms, deep webs and low gill counts (4–5 *v.* 4–6). However it is clearly delineated by the nature of the radula (complete and highly modified *v.* the degenerate form of *Thaumeledone*). *Microeledone* also differs in funnel organ (a distinct deep UU *v.* the narrow and shallow VV or IIII of the two *Thaumeledone* species) and smooth skin (*v.* papillose).

The generic placement of O'Shea's species *T. marshalli* and *T. zeiss* require further consideration and await a more thorough description of the core characters of radula structure and attributes of the digestive systems for these two species. Full descriptions of

the mature reproductive systems of all taxa are also required. It is clear that the genus *Thaumeledone* requires a thorough revision.

Biogeography

Geographic and vertical distributional patterns may provide clues into the phylogenetic affinities of the new genus. Amongst the octopodid genera that possess a single row of suckers, the majority of genera and species occur in two regions:

(*1*) Temperate and tropical latitudes of the Atlantic Ocean: all *Eledone* species (except '*Eledone*' *palari* Lu and Stranks, 1992, see comments below); *Tetracheledone* and *Vosseledone*.

(2) Antarctic and subantarctic waters: *Pareledone, Megaleledone, Adelieledone, Bentheledone* and *Thaumeledone.*

The genus *Graneledone* is scattered throughout the world's oceans: primarily in the northern Pacific Ocean, north-west Atlantic Ocean, southern Pacific and Indian Oceans, and Antarctica (Voight 2000). The species that have been placed in *Graneledone* need to be critically re-evaluated to determine if more than one genus is represented. The two remaining uniserial genera have more restricted distributions. *Velodona togata* Chun, 1915 occurs at tropical latitudes in the western Indian Ocean. '*Eledone*' *palari* occurs on the continental slopes around Australia and in southern Indonesia. It's placement within the genus *Eledone* has been questioned (Norman *et al.* 1997) and is the topic of current research (Hudelot, Boucher-Rodoni and Hochberg unpublished data).

Microeledone is closest in form to species placed in the genera *Thaumeledone*, *Bentheledone* and *Graneledone*. These genera, the closest geographically to *Microeledone*, also occur at the greatest depths amongst those octopuses with a single row of suckers. Depth information provided below comes from Voss (1988*a*, 1988*b*), Voss and Pearcy (1990), Lu and Stranks (1992, 1994), O'Shea (1999) and Norman and Hochberg (unpublished data).

Microeledone was trawled from 980–1000 m deep. *Thaumeledone brevis* has been recorded between 800 and 3931 m, while *T. gunteri* is known only from the female holotype collected from 410 m. O'Shea's new species were captured from depths over 1000 m: *T. marshalli* 1999–2542 m; *T. zeiss* 1052–1386 m. *Bentheledone rotunda* (Hoyle, 1885) was collected from 3596 m and *B. albida* (Berry, 1917) from 3111 m. A specimen of an undescribed species of *Bentheledone* also has been collected at a depth of 3475 m off Peru (Cardosa and Hochberg unpublished data). Except for *Graneledone gonzalezi* Guerra, González and Cherel, 2000 found at depths of 200–950 m in the subantarctic Indian Ocean (Heard Island), all records of the seven or more species of *Graneledone* are from 477–2756 m deep.

The Antarctic genera with a single row of suckers show wider depth ranges, extending from shallow depths into deeper waters (e.g. *Pareledone* 15–1116 m; *Megaleledone* 120–761 m). This may reflect the absence of temperature thermoclines in polar latitudes. The remaining genera with a single row of arm suckers are from shallower waters: *Eledone moschata* (Lamarck, 1798) (< 300 m), *E. cirrhosa* (Lamarck, 1798) (10–800 m), *E. caparti* Adam, 1951 (60–170 m), *E. massyae* Voss, 1964 (73 m), '*Eledone*' *palari* Lu & Stranks, 1992 (110–620 m), *Vosseledone charrua* (10–200 m), *Tetracheledone spinicirrus* Voss, 1955 (183–544 m) and *Velodona togata* Chun, 1915 (290–749 m).

It is unknown whether the morphological similarities between *Microeledone* and the other three deeper genera (*Graneledone, Thaumeledone* and *Bentheledone*) constitute

evidence of shared evolutionary history or are instead habitat-related convergences in form. Voss (1988*a*) suggested many characters of deep-water octopuses related to their environment. The following of Voss' characters are found in this suite of deep-water taxa with a single row of suckers: loss of ink sac, loss or reduction of crop diverticulum, reduction in number of gill lamellae and marked extension of the web. Insights into the influence of phylogeny *v.* convergence (due to habitat) will not be possible until better reference material is obtained, more detailed morphological descriptions are produced for all groups, and several phylogenetic studies based on molecular characters that are currently in progress are completed.

The single specimen of *Microeledone mangoldi* was collected through the MUSORSTOM surveys of seamounts and deep habitats in tropical latitudes of the Pacific Ocean. These surveys encountered many rare and unusual forms including numerous taxa previously thought extinct (see Richer de Forges 1990). At this stage there are limited insights offered by a single specimen of this new taxon; however, the distinctive radula of this octopus is unlike any previously reported. Four other new genera are currently being described from deep waters in this south-west corner of the Pacific Ocean (works in progress). With so many weird and wonderful animals coming to light, it is an exciting time for octopus systematics.

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Appendix 1. Additional material examined

Bentheledone rotunda (Hoyle, 1885)

Holotype. 1F (immature and poor condition): total length ~150 mm, Southern Ocean, 53°55′S, 108°35′E, 1950 fms, 3 Mar. 1874, coll. Challenger Expedition (BMNH 1890.1.24.6).

Eledone cirrhosa (Lamarck, 1798)

1M (mature): 74.4 mm ML, Delante de Barcelona, Spain, 41°23′N, 2°11′E, 180 m, 12 Nov. 1978, coll. E. Morales (USNM 730592).

Eledone moschata (Lamarck, 1798)

1M (mature): 77.1 mm ML, Gulf of Tunisia, 36°57′N, 10°28′E, 64–75m, 30 Mar. 1967 (USNM 577099).

Tetracheledone spinicirrus Voss, 1955

1M (mature): 71.9 mm ML, Off Oregon, Stn 1547, 24°28′N, 83°30′W, 210 fms, 17.VI.1956 (MRHNB IG 22810).

Thaumeledone brevis (Hoyle, 1885)

Syntypes. 3F (immature), largest 20 mm ML, south Atlantic Ocean, off Monte Video (off mouth of Rio de la Plata), 37°17′S, 53°52′W, 600 fm (1097 m), 14 Feb. 1876, coll. H.M.S. Challenger, station 320, trawl, green sand (BMNH 89.4.24.50–1).

Thaumeledone gunteri Robson, 1930

Holotype. **Antarctica:** 1F (mature), 34 mm ML, (Scotia Sea, NE of South Georgia Island), 53°48.5′S, 35°57.1′W, 401–411m (219–224 fm), 21 Jan. 1927, coll. R/V Discovery, station 158, large dredge (net DLH), rock bottom (BMNH 1951.4.26.50); 1F (mature), 39 mm ML, off Enderby Land, 66°03.0′S, 49°50.0′E; 690–911 m; 29 Nov. 1985, coll. M. D. Norman, ANARE, M/S Nella Dan, station HRD-013, epibenthic sled, through sea-ice (MV F65706); 1F (mature), 50.5 mm ML, 1M (immature), 38.5 mm ML, 62°11.3′S, 42°43.3′W, 1228–1400 m; 20 Feb. 1976, coll. USARP/SOSC, R/V Islas Orcada, cruise 876, station 117, 10 ft Blake trawl (USNM 817378). South Shetland Islands: 1M (mature), 37mm ML, 1M (immature), 23.7 mm ML, 1F (submature), 23.8 mm ML, 62°00′S, 61°09′W, 0–1437 m; 8 Aug. 1962, coll. Johnson, Matsudo, J. Mohr & J. Paxton, R/V Eltanin, station USC-138, 10 ft Blake trawl (USNM 817371).

Velodona togata Chun, 1915

1M (mature), 94.0 mm ML, off Mozambique, 16°20.0′S, 40°8.0′E, 500 m, 16 Jun. 1994 (SAM S3061).

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New Taxon

Description of *Austrodevonia sharnae* n. gen. n. sp. (Galeommatidae : Bivalvia), an ectocommensal of *Taeniogyrus australianus* (Stimpson, 1855) (Synaptidae : Holothuroidea)

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Abstract

Austrodevonia sharnae n. gen. n. sp. is an ectocommensal on the sand dwelling holothurian *Taeonigyrus australianus* (Stimpson, 1855) in the intertidal zone in the vicinity of Sydney, New South Wales, Australia. The species adheres by way of a dorsoventrally flattened foot and byssus, and is located predominantly medioventrally on the holothurian. The species is compared with other galeommatoidean taxa that coexist with holothurians, i.e. *Devonia*, *Anisodevonia*, *Benthoquetia*, *Entovalva*, *Scintillona* and *Cycladoconcha*.

Introduction

Several bivalve taxa are known to live in commensal or parasitic relationships with holothurians. Some live in the digestive tract of the holothurian, while others live attached to the exterior integument of burrowing species. Kato (1998) noted similarities between endo- and ectocommensal species. A short review of the bivalves found in association with holothurians is provided here.

The earliest record of ectocommensal bivalves on holothurians was Semper's (1868) brief record of a bivalve adhering to *Bohadschia similis* (Semper, 1868) in the Philippines (Ohshima 1930; Boss 1965) and a possible conspecific, *Devonia semperi* (Ohshima, 1930) (Fig. 1*b,c*), subsequently found on the holothurian *Protankyra bidentata* (Woodward & Barrett, 1858) in Japan by Ohshima (1930). The first comprehensive description of ectocommensal bivalves on holothurians was Malard's (1903) description of the European *Devonia perrieri* (Malard, 1903) (Fig. 1*a*) from northern France. Malard noted the presence of up to three specimens of *D. perrieri* attached to the skin of *Leptosynapta inhaerens* (O. F. Müller, 1776) by means of byssus and crawling on the skin with the aid of a very large expanded foot. *Devonia perrieri* has subsequently been recorded throughout northern Europe (Johannessen and Wikander 1976). A record of *D. perrieri* from the western Atlantic (Clench and Aguayo 1931) is likely erroneous as the shells of the species described are not covered by the mantle (and is thus more like the new genus and species described here). An additional ectocommensal species, *Devonia ohshimai* Kawahara, 1942 (Fig. 1*d,e*), was described from Japan on *Patinapta ooplax* (von Marenzeller, 1881) and is now type species of the genus *Anisodevonia* Kato, 1998.

Other galeommatoidean taxa adhering to holothurian integument include *Scintillona zelandica* (Odhner, 1924) (type of *Scintillona* Finlay, 1927) from New Zealand living attached to *Trochodota dendyi* Mortensen, 1925 (Finlay 1927) and *Scintillona bellerophon* Ó Foighil & Gibson, 1984 from British Columbia living on *Leptosynapta clarki* Heding, 1928 (Ó Foighil & Gibson, 1984). Both species of *Scintillona* use the lateral side of the foot

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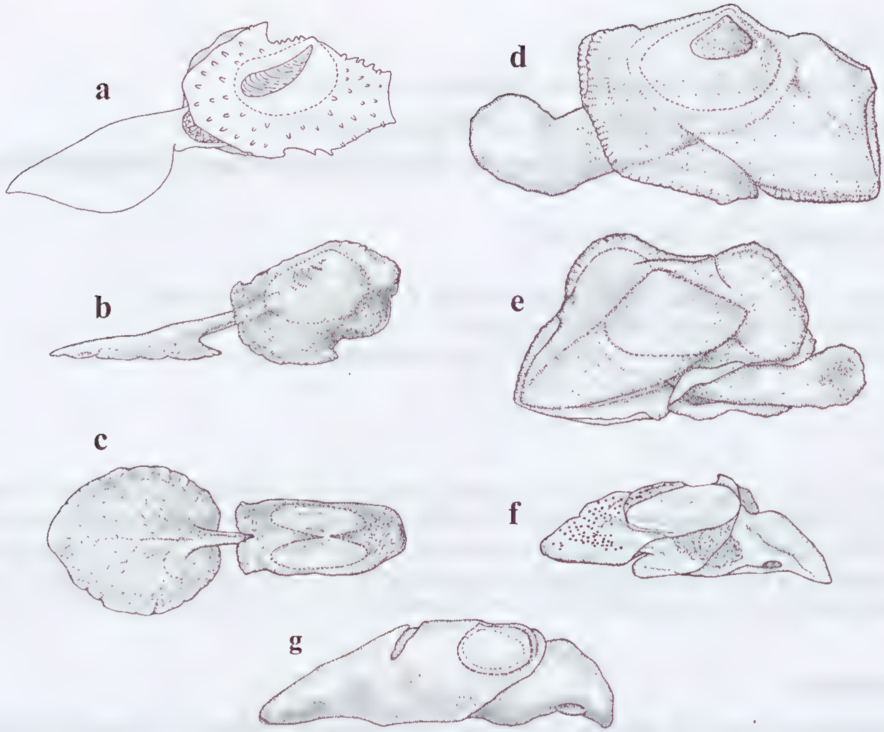

Fig. 1. (*a*) *Devonia perrieri* (Malard, 1903) reproduced from Anthony (1916, fig. 3), length ~8 mm; (*b,c*) *Devonia semperi* (Ohshima, 1930, pl. 2, figs 3, 4), length ~20 mm; (*d,e*) *Anisodevonia ohshimai* (Kawahara, 1942, text figs 1, 2), length ~6 mm; (*f*) *Entovalva mirabilis* Voeltzkow, 1898 reproduced from Schepman and Nierstrasz (1914, pl. 30, fig. 63), length ~5 mm; (*g*) *Cycladoconcha amboinensis* Spaerck, 1932, (fig. 2), length ~7.5 mm. All lengths are of whole animal, measured from the original illustrations and reproduced from original illustration unless otherwise stated.

for locomotion (like the ectocommensal *Anisodevonia* and the endoparasitic *Entovalva* Voeltzkow, 1891 and *Cycladoconcha* Spaerk, 1932) and adhere with a posterior pedal byssus to the host (Ó Foighil and Gibson 1984). Finally, *Benthoquetia* Iredale, 1930 (type species *Turquetia integra* Hedley, 1907), is known to cluster around the anus of the holothurian *Mesothuria lactea* Théel, 1886 in south-east Australia and New Zealand (Ponder 1968).

Two endocommensal galeommatoidean genera are know to inhabit the oesophagus of holothurians: *Entovalva* from east Africa (type *E. mirabilis* Voeltzkow, 1891; Fig. 1*f*) and *Cycladoconcha* (type species *C. amboinensis* Spaerck, 1932; Fig. 1*g*) from Indonesia. Additional species of *Entovalva* are known from the Red Sea (Bruun 1938), Japan (Kato 1998) and Australia's Great Barrier Reef (P. Middelfart unpublished data).

Besides records of *Benthoquetia integra* there are no published species descriptions of galeommtoideans living in association with holothurians in Australia, except for one photo in Coleman (1981, 2003) of a galeommatid adhering to the holothurian *Chirodota* in Western Australia.

This paper is part of a two-part study into the systematics of galeommatoidean bivalves associated with holothurians. The second part will focus on the endocommensal species, *Entovalva s.l.*

Materials and methods

Material used in the paper was collected alive from Long Reef, north Sydney, New South Wales in 2003 and deposited in the Australian Museum, Sydney (AM) and Muséum National d'Histoire Naturelle, Paris (MNHN). Additional previously collected material in the AM was also examined. Live specimens were removed from their valves, dyed in methylene blue, examined using a stereo microscope at 25–50× magnification and drawn with the aid of a camera lucida. The shells were mounted on stubs, gold coated, examined in a LEO s.e.m. and photographed digitally. Shell length, height, inflation and prodissoconch length were measured with an ocular ruler on a stereo microscope.

Systematics

GALEOMMATOIDEA Gray, 1840

GALEOMMATIDAE *sensu lato* (Beesley *et al.*, 1993)

Austrodevovia n. gen.

Type species: *Austrodevonia sharnae* n. sp.

Differential diagnosis

Species of *Devonia* Winckworth, 1930 are most similar to *Austrodevonia*, but differ in a few very important aspects. First, the mantle of *Austrodevonia* only covers the shells marginally antero- and posterodorsally. Second, the hinge of *Austrodevonia* is more like that of species of *Montacuta s.s.*, including the presence of one large down-turned anterior cardinal in the right valve and a small anterior cardinal in the left valve. *Devonia* is entirely toothless and the hinge resembles *Entovalva s.s*. Additional differences include: ventral gape between valves, tentaculate mantle of *D. perrieri* (Fig. 1*a*) covering a larger part of the shell and almost enclosing it, and an extended anterior mantle and a posterior exhalant chamber (which also serves as a brood chamber). It is interesting to note that despite the obvious morphological differences from *Devonia*, *Austrodevonia* have a very similar foot, gill and palp structure, with no major differences observed here (for details of *Devonia* see Popham 1940, figs 20, 21). *Anisodevonia* and *Entovalva* may be separated from *Austrodevonia* in being bilaterally asymmetrical with a lateral right byssus gland on the foot and having dysodont fragile shells. *Cycladoconcha* is asymmetrical like *Entovalva*, but differs in that the central dissoconch is dissolved with only a shell-ring remaining. The ectocommensal *Benthoquetia* differs most markedly in the simple laterally flattened foot and in shell characters (see Ponder 1968). Species of *Scintillona* differ from *Austrodevonia* in many characters such as external shell structure, the laterally flattened foot with distal ciliated grooves, and in having inner and outer demibranchs.

Etymology

The genus name, *Austrodevonia*, is derived from the Latin 'austro', meaning 'southern', and the genus name *Devonia*, literally meaning 'the southern *Devonia*'.

Austrodevonia sharnae n. sp.

(Figs 2–4; Table 1)

Material examined

Holotype. New South Wales, Sydney N., Collaroy, Long Reef, Fishermans Beach, 33°44.3′S, 151°18.6′E, 17 Apr. 2003 (AM C.205093) (ex. AM C.205062). Measurements: dissoconch: 3.04 mm long, 2.48 mm high, 1.22 mm inflation (both valves); prodissoconch: 0.44 mm long.

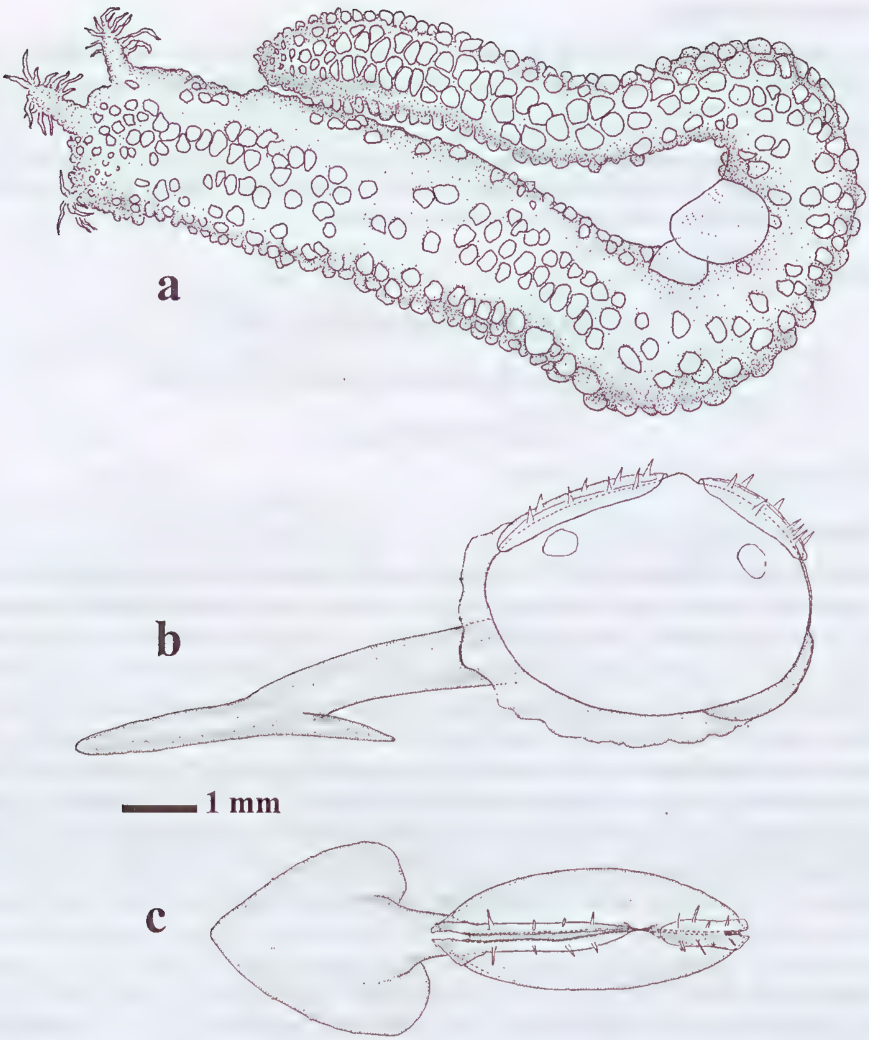

Fig. 2. *Austrodevonia sharnae* n. sp. (*a*) attached to integument of *Taeniogyrus australianus* (AM C.126713); (*b*) left side aspect of living animal with foot extended; (*c*) dorsal aspect with foot slightly contracted (*b* and *c* drawn from AM C.205062).

Paratypes. **New South Wales:** Sydney N., Collaroy, Long Reef, Fishermans Beach, 33°44.3′S, 151°18.6′E, in gutter: 8 specimens, 8 Mar. 1981 (AM C.126713); 1, 13 Apr. 1980 (AM C.205061); 1, 19 Sep. 1979 (AM C.428576); 2, 29 Jan. 1979 (AM C.428582); 1, 25 Sep. 1977 (AM C.428586); 14, 17 Apr. 2003 (AM C.205062); 2, 17 Apr. 2003 (MNHN); 4, 15 Oct. 1977 (AM C.107868), 2, 8 Jan. 1978 (AM C.428574); 1, 19 Aug. 1978 (AM C.428578); 7, 14 Jan. 1979 (AM C.428580).

Other material examined. **New South Wales:** 3, N. of Woolgoolga, Arrawarra, 30°4′S, 153°12′E, 13 Mar. 1982 (AM C.400904); 2, N. of Cronulla, Boat Harbour, 34°2.5′S, 151°12′E, 3 Nov. 1982 (AM C.428577).

Description

Shell (Fig. 3). Largest specimen measured 4.4 mm long, 3.3 mm high (n = 39). Smallest specimen observed 1.2 mm long. Valves white to translucent, broadly oval, equivalve,

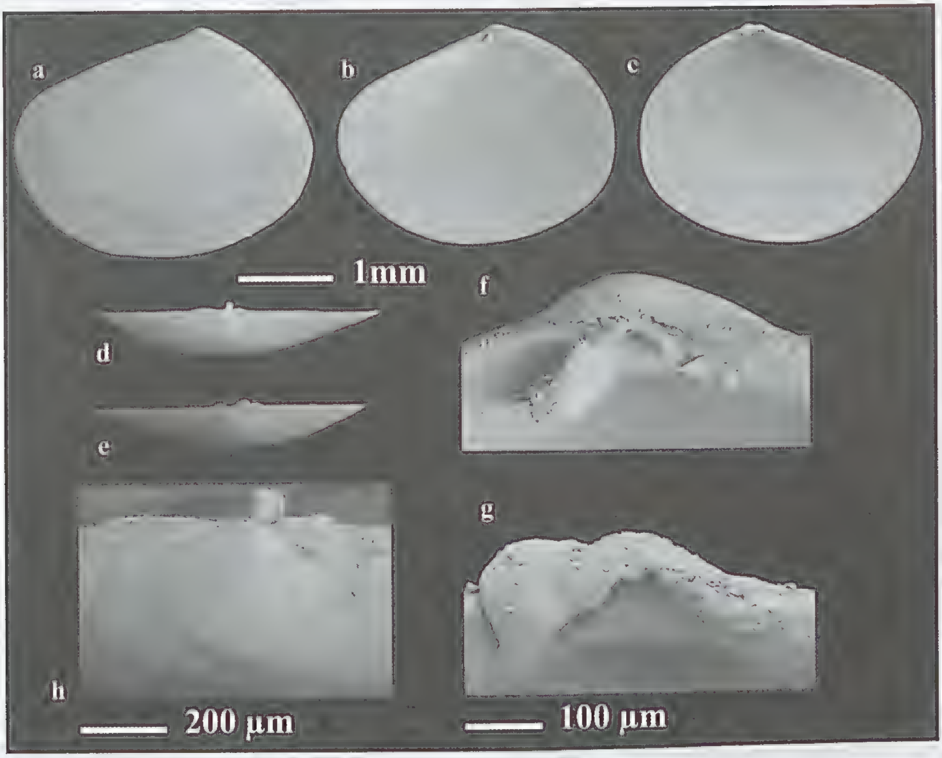

Fig. 3. *Austrodevonia sharnae* n. sp. (AM C.205062). (*a*) left valve; (*b,d,f,h*) right valve in interior, dorsal, hinge and prodissoconch aspects; (*c,e,g*) left valve in interior, dorsal and hinge aspect.

inequilateral, with orthogyrous umbo slightly posterior, anterior end extended and rounded. No gape between valves. Cardinal teeth consist of anteroventral directed elongate cardinal tooth (CA3b), slight rim near edge (CA3a) in right valve. Left valve with anteroventral direct elongate-triangular cardinal tooth (CA2a). Posterior cardinal lacking. Elongate lateral teeth present on anterior dorsal slope in right (LA1) and left (LA2) valves. Periostracum not visible, ligament internal in resilium. Surface smooth with weak commarginal growth rings. Prodissoconch oval, 0.3–0.46 mm in length (0.38 mm ± 0.05 mm, X ± s.d., $n = 16$, AM C.205062).

Animal (Figs 2, 4) with large anterior opening, consisting of laterally flared middle mantle fold expanded to narrow cowl, extending posterior past median line. Posterior exhalant opening small; among small tentacles of the middle mantle fold. Mantle fusion between inhalant and exhalant openings slightly extended beyond shell edge to accommodate demibranchs when inflated (gill pouch). Antero- and posterodorsal middle mantle with about eight paired tentacles anterodorsal and posterodorsal. Foot very large, dart-shaped, and dorsoventrally flattened to form wide sole. Anterior end pointed, posterior end with two lateral rounded flaps. Byssus gland on distal part of cordiform foot shaft. Only inner demibranch present. Cilial currents on inner and outer lamellae direct food ventrally. Ventral food groove directs food string anteriorly to small paired labial palps. Adductors small and isomyarian, paired anterior and posterior pedal retractors observed.

Table 1. ***Austrodevonia sharnae*** **n. sp., measurements of material examined**

Type	Shell length (mm)		Shell height (mm)		Shell width (mm)		Prodissoconch length (mm)	
	Range	Mean ± s.d.	Range	Mean ± s.d.	Range	Mean ± s.d.	Range	Mean ± s.d.
A. sharnae holotype C.205093	3.04	–	2.48	–	1.22	–	0.44	–
A. sharnae all paratypes from Long Reef, Sydney ($n = 33$)	1.16–3.92	2.52 ± 0.60	0.76–2.75	1.87 ± 0.41	0.42–1.30	0.93 ± 0.24	0.30 – 0.46	0.38 ± 0.05
A. sharnae, C.400904 ($n = 3$)	1.58–2.67	2.11 ± 0.54	067–1.92	1.36 ± 0.64				
A. sharnae, C.428577 ($n = 2$)	3.08, 4.42	–	2.67, 3.33	–				

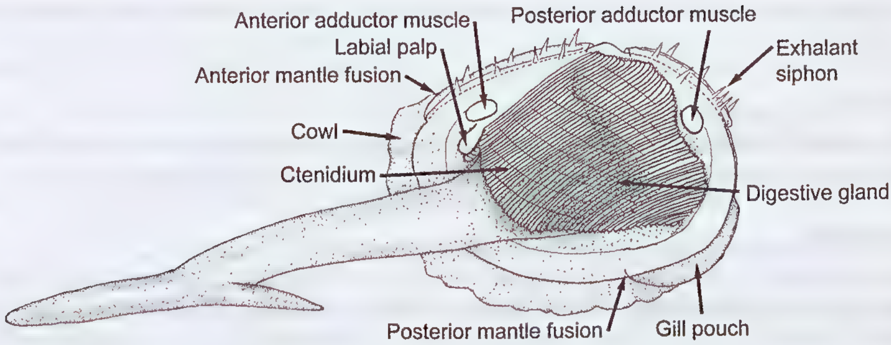

Fig. 4. *Austrodevonia sharnae* n. sp. (AM C.205061), anatomy.

Association

The association of *A. sharnae* with *T. australianus* (see Fig. 2*a*) was studied in some detail in a small habitat on the northern side of Long Reef, Sydney. A total of ten clusters of sea cucumbers were found under large rocks and examined in the laboratory within hours of capture. An average of two holothurians (range 1–4, total 20 specimens) were found under each of the inhabited rocks, in the sand. The holothurians were only found where this microhabitat was present.

Of the 20 holothurians examined, 16 (80%) had bivalves attached to the integument and of these, four had two specimens attached (the remaining had one specimen attached). The position and direction of the bivalves were observed in 12 holothurians with a total of 16 bivalves attached. Eight specimens (50%) were arranged with the anterior end of the bivalve pointing anteriorly on the holothurians, six (37.5%) were directed across or obliquely across and two (12.5%) pointing posteriorly. Seven specimens (43.75%) were located medially on the holothurian, four (25%) near the anterior 1/3 of the holothurian, two (12.5%) near the posterior 1/3, two (12.5%) on the posterior end and one (6.25%) on the anterior end. Fifteen (93.75%) were located on the ventral side of the holothurian, while one specimen was located on the lateral side. In conclusion, the preferred location on the host seems to be approximately medioventrally on the holothurian, with the anterior end of the bivalve facing anteriorly on the host.

Distribution

This species has only been recorded from the north and central NSW coasts, but detailed searches in other parts of NSW have not been undertaken.

Remarks

The structure and cilial patterns of this species closely resemble those illustrated and discussed in Popham (1940) for *Devonia perrieri*; probably an indication of close relationship.

One additional record of a species resembling *Austrodevonia* exists from Gun Island, Houtman Abrolhos, Western Australia (Coleman 1981: 83, fig. bottom left; Coleman 2003: 77, lower left). This species appears to be more elongate than *A. sharnae* as far as can be judged from the figure, but specimens have not been examined. The host, which is cited as *Chirodota* in Coleman (1981), is different from the host *T. australianus* in NSW, but that is

not in itself an indication that they are separate species (see Johannessen and Wikander 1976).

Etymology

This species is named after Ms Sharn Rose, a dedicated volunteer at AM, in appreciation of the many illustrations she has prepared for projects on small marine bivalves.

Discussion

Austrodevonia sharnae, as shown here, seems to be distinct from other ecto- and endocommensal galeommatoideans when shell and soft-part morphological characters are used in conjunction. Molecular studies are currently underway and it is hoped that the molecular data will enhance our understanding of the phylogenetic position of this species.

In a recent paper of the ecology of *A. ohshimai* from southern Japan (Kosuge 2001), the prevalence and abundance of the species on *P. ooplax* was studied. The prevalence of bivalves was close to the rate found at Long Reef (67–72% in southern Japan *v.* 80% at Long Reef). While the abundance of *A. sharnae* on *T. australianus* varies from one to two specimens (80% of hosts with one specimen), *P. ooplax* may have up to eight specimens attached, with up to five being more frequent. It is puzzling why more specimens are attached to *P. ooplax* than *T. australianus* as the size range of the host and bivalve is closely similar. It is possible that the prevalence is a result of the higher abundance of *P. ooplax*, resulting in more available substrate for settling larvae.

Only a very small part of the Australian coastline has been investigated for commensal bivalves living in association with echinoderms. With the rich echinoderm fauna of Australia it is very likely that many more interesting species and associations will be found in the future.

Acknowledgments

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